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NAME OF SUPERVISOR/NOM DU DIRECTEUR DE THÈSE DR. GEORGE H. La Roi

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THE UNIVERSITY OF ALBERTA

VEGETATION OF THE VINE CREEK DRAINAGE BASIN, JASPER NATIONAL PARK

by

LOREN ROBERT HETTINGER (C)

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

IN PLANT ECOLOGY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Vegetation of the Vine Creek drainage basin, Jasper National Park" submitted by Loren Robert Hettinger in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Plant Ecology.

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Supervisor

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.....
External Examiner

Date ...29...October...1975

ABSTRACT

Thirteen habitat types of five Series representing zones in a climatic gradient were described from 35 quantitatively sampled stands. Habitat types were designated using cluster analysis, two-dimensional ordination and tree size distribution characteristics for indication of potential climax. Habitat types included: *1) Arctostaphylos uva-ursi - Calamagrostis purpurascens* (montane scrubland), *2) Pseudotsuga menziesii/ Juniperus communis/Calamagrostis purpurascens, 3) Pseudotsuga menziesii/ Elymus innovatus, 4) Picea glauca/Carex vaginata - Linnaea borealis, 5) Picea glauca/L. borealis - Hylocomium splendens, 6) Picea glauca/E. innovatus - Cornus canadensis, 7) Picea glauca/Alnus crispa/E. innovatus, 8) Picea - Pinus albicaulis/J. communis/ E. innovatus, 9) Picea engelmannii - Abies lasiocarpa/Menziesia glabella - Vaccinium membranaceum, 10) Picea engelmannii - Abies lasiocarpa/Arnica cordifolia, 11) Picea engelmannii - Abies lasiocarpa/Arnica divereifolia/Hylocomium splendens, 12) Salix glauca/E. innovatus, 13) Salix vestita/Poa alpina.*

A warm-dry to cool-mesic climatic gradient was observed, using a series of weather stations, which followed an increase in elevation. This gradient was followed by a distinct arrangement of plant communities from montane to subalpine. Abrupt changes in the gradient steepness were indicated by vegetation heterogeneity. This climatic gradient was also reflected by a shift from *Picea glauca* to *Picea engelmannii* with elevation increase, with a hybrid swarm occurring at mid-elevations.

A number of landform, soil and habitat type relationships were evident, but these were strongest at the Series and Soil Order levels. Habitat types were most closely related to climatic variables. Fire history complicates some vegetation - environmental relationships, and also the vegetation pattern.

Many of the montane h.t.s exhibited affinity to boreal communities, whereas those of the subalpine were more closely related to Cordilleran and Pacific communities to the south and west. Within the montane zone however, *Pseudotsuga* h.t.s were indicated as having a stronger Cordilleran affinity, whereas those of *Picea glauca* had a stronger boreal affinity.

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I. INTRODUCTION

Studies on the vegetation of the Rocky Mountains date primarily from the turn of the century (Daubenmire 1938, 1943a; Heusser 1956). Interest in the region has been aroused by the sharp visual contrast in the mountain and surrounding plain vegetation, the obvious compression of vegetation types into a relatively small area along an elevation gradient and the continuous nature of the Cordillera which ranges latitudinally across most of North America. Some of this area, especially within Alberta, still contains vegetation which has not been affected greatly by man's activities. This is due in part to the establishment of national parks which have only recently been traversed by road systems, and much of the area within Banff and Jasper is still accessible only by trail. Thus the national parks contain the closest present example of naturally evolved landscape systems and form a baseline to which high-use areas can be referenced.

Recognition of the importance of natural areas to an understanding of ecological relationships and land use planning has led to a number of vegetation studies. Those within Jasper National Park have concentrated primarily on particular vegetation zones, community types and floras (Beil 1966, Hnatiuk 1969, Hrapko 1970, Stringer & La Roi 1970, Laidlaw 1971, Stringer 1973, Kuchar 1975). Thus the need was established for a more integrated regional study investigating the range of plant communities in order to document their interaction and response to environmental factors. The Vine Creek drainage basin in Jasper National Park was

chosen for such a study since the area was considered of manageable size for field work, contained a landscape representative of the Front Range of the Rocky Mountains and was definable on a geographic basis and could thus be treated as a reasonably independent system of interacting components. A study using the above guidelines was considered important in understanding natural relationships between the biotic and abiotic components of Rocky Mountain landscape systems in order to formulate and implement efficient management policies.

Field work was initiated in 1970 in order to meet the following objectives: (1) To describe the composition, structure and dynamics of the vegetation; (2) To describe the major landform features as they relate to the vegetation pattern; (3) To ascertain the influence of a number of environmental factors on plant community distribution; and (4) To investigate meteorological conditions along an elevation gradient according to different community types.

II. LITERATURE REVIEW

A. VEGETATION ZONATION

Vegetation of mountainous regions is often referenced to elevational belts or life zones which originated with the concepts of Merriam (1898). Rydberg (1915) recognized alpine, subalpine, montane and foothills zones, and this nomenclature has been widely used to the present. Daubenmire (1943a) designated alpine tundra, needle-leaved forest and grassland or desert formations as the major physiognomic regions of the Rocky Mountains. Various zones were recognized especially within the needle-leaved forest formation and characterized by Engelmann spruce-alpine fir, Douglas fir, ponderosa pine and juniper-pinon forests. Variation in the composition of the formations and zones along a latitudinal gradient was recognized, and Southern, Central, Northern and Far-Northern provinces were designated (Daubenmire 1943a). The line between the Northern and Far-Northern provinces occurs at about 50°N in Alberta and British Columbia, and thus the study area falls within the latter province. Beil (1966) thought that the separation between the two northern provinces was gradual on the basis of black spruce distribution, and that much of Alberta was a transition area. Ogilvie (1960) noted that a trend from mainly cordilleran to increasing boreal elements occurs through the Banff and Jasper area with increasing latitude.

Stringer and La Roi (1970) designated alpine, spruce-fir and Douglas fir zones for the Alberta Rockies, the lower (ponderosa) zone being absent above 47°N. Kuchar (1973) indicated that zonation in Waterton

National Park was not distinct, with the effect of irregular topography and aspect having a disruptive influence. Previous investigations have found compositional differences within the zones between Jasper and Banff National Parks. According to Oosting (1956) the basal plains of the far-northern province are frequently above the upper elevational limit of the montane forest as reflected by the discontinuous nature of Douglas fir. Yet, grasslands are found sporadically in the valleys of both Jasper and Banff National Parks with a *Koeleria - Calamagrostis* association the most prominent type in the Athabasca River Valley of Jasper (Stringer 1973). The *Festuca scabrella* association of the aspen parklands to the east, and elements of the *Agropyron spicatum* grasslands of British Columbia were also designated for the area (Moss 1955).

The basal plains of Jasper National Park contain, in addition to grasslands, a forest mosaic of mainly white spruce *(Picea glauca)*, lodgepole pine *(Pinus contorta* var. *latifolia)* and Douglas fir *(Pseudotsuga menziesii* var. *glauca)* (La Roi 1967, Hnatiuk 1969, Stringer & La Roi 1970). Black spruce *(Picea mariana)* occurs as a minor component of the vegetation in the lower valleys of Jasper, around some lakes and on relatively old alluvium of stream courses (Laidlaw 1971). The species also occurs at higher elevations in what Laidlaw (1971) described as "hangmoor" peatland, and in lodgepole "wetland", as well as in spruce-fir communities. Aspen *(Populus tremuloides)* and balsam poplar *(Populus balsamifera)* form small stands within the montane zone (Moss 1932). The occurrence of balsam poplar is more restricted than aspen, being found primarily on course alluvium, but both are associated with depositional

disturbances. Although most of the Alberta work on these two species has been done in the boreal forest and aspen parkland regions, Moss (1955) found sufficient similarities in the montane aspen groves of SW Alberta to classify them as a variant of the central Alberta consociations.

White spruce increases in abundance within the montane zone with increase in latitude through the far-northern province. This increase is due to an increasing boreal influence which is also accompanied by an abundance of other species that are common across Northern Alberta (Halliday & Brown 1943, Porsild 1951, Moss 1955, Hulten 1968). White spruce forms a montane mesophytic forest type and is also found on young river terraces and ravine bottoms of the Athabasca River Valley in Jasper (Stringer & La Roi 1970). La Roi (1967) found similar floristic characteristics for white spruce stands in Jasper and north central Alberta. White spruce extends south into Banff National Park and from the east into Jasper where it is eventually replaced by Engelmann spruce *(Picea engelmannii)* at higher elevations (Moss 1955). Introgressive hybridization between white and Engelmann spruce is well documented (Horton 1959, Beil 1966, La Roi & Dugle 1968, Daubenmire 1974) and creates some problems in species identification. White spruce was not designated by Cooper (1916) as an associate of the montane forest on the west slope of the Rocky Mountains near Mt. Robson, but intergradation between Engelmann and white spruce was probably not recognized at this time.

White spruce communities appear to be prominent south of Jasper National Park through Banff (Ogilvie 1962), the Crowsnest Forest Reserve (Cormack 1956) and Waterton (Kuchar 1973). A number of communities dominated by spruce have also been identified in Montana (Pfister *et al.* 1974). In many of the above areas white spruce was found in the more mesic habitats in relation to Douglas fir or ponderosa pine. The species was not listed as a dominant of the lowland forests on the western slope of N Montana (Habeck 1963, 1968).

White spruce has been characterized as typifying a boreal subzone in east central British Columbia (Krajina 1969) where it forms a number of community types (Wali & Krajina 1973). In these areas white spruce occurs primarily along the base of valleys, and as in Alberta, becomes more abundant with increase in latitude (Tisdale & McLean 1957, Illingworth & Arlidge 1960). McLean and Holland (1958) noted that white spruce became more prominent in the Douglas fir zone N of Brisco (51°N), and Garman (1957) found it forming a number of community types in NE British Columbia. White spruce replaces Engelmann spruce N of about Prince George, B.C. (ca 54°N; Alexander 1958a) and forms the basis of the subalpine zone through the remainder of the far-northern province into arctic areas (Raup 1947, Daubenmire 1953, Hettinger & Janz 1974).

Douglas fir occurs in Jasper National Park on warm S exposed slopes and rocky ridges to about Brule Lake (53°15'N, 119°30'W; Stringer & La Roi 1970). Variation in topography of sites and fire history has caused a number of different community types, although only two dry-

mesophytic climax types were recognized in the Jasper-Banff area (Stringer & La Roi 1970). Douglas fir has been widely used as a characteristic feature of the montane zone since it extends throughout most of the Rocky Mountains in the United States. Douglas fir occurs as a major species of the montane zone in the Crowsnest and Waterton Lakes area in S Alberta (Cormack 1956, Jeffrey *et al.* 1968, Kuchar 1973). The species becomes quite extensive at lower elevations throughout the mountains of N Idaho and Montana where a number of climax associations have been recognized (Larsen 1930, Habeck 1967, Daubenmire & Daubenmire 1968).

The Douglas fir forests of interior British Columbia typify a fairly xeric area of the Canadian Cordilleran Forest Region (Krajina 1965). The importance of Douglas fir in the interior of British Columbia is reflected in the number of studies which have described and characterized a number of component community types. Two subzones, the arid groveland and forest have been recognized in the S portion of the province (McLean & Holland 1958). Tisdale and McLean (1957) recognized several associations for this area, but lodgepole was the dominant tree in many of the communities. Nine site types were identified for the Douglas fir zone in the Caribou-Moneshee Mountain Range near Kamloops, but again lodgepole was the dominant overstory species (Illingworth & Arlidge 1960). Brayshaw (1965) and McLean (1970) together recognized five associations for the S interior of British Columbia. Douglas fir extends north to at least Prince George, but pure stands appear to be infrequent, due probably to past fires (Tisdale & McLean 1957).

Lodgepole pine is abundant throughout the far-northern, as well as northern provinces of the Rocky Mountains to about 63°N, as a result of past fires (Bloomberg 1950, Cormack 1953, Hulten 1968). According to Horton (1955), lodgepole pine is also dominant in the foothills where white spruce - alpine fir vegetation is the climax, as well as at higher elevations where fire has occurred in the Engelmann spruce - alpine fir zone. Hnatiuk (1969) recognized a number of lodgepole pine forest types in Banff and Jasper according to subordinate strata differences which were then separated according to habitat on the basis of moisture conditions. Smithers (1961) noted that different lodgepole pine habitat types could be separated on a general basis according to landform materials and moisture conditions, but did not elaborate on understory composition. The Athabasca River Valley of Jasper contained mostly xerophytic associations (Hnatiuk 1969).

Lodgepole pine is abundant throughout the foothills north of Jasper (Smithers 1961, Corns 1972) and also forms extensive forests along the E slopes and foothills adjacent to the national parks (Horton 1955), and to the south through the Crowsnest Pass into Montana (Bloomberg 1950, Cormack 1953, Jeffrey *et al.* 1968, Pfister & Daubenmire 1973). Lodgepole is also a common seral species to the west in the interior of British Columbia in both the ponderosa pine and Douglas fir zones (Tisdale & McLean 1957, McLean & Holland 1958, Illingworth & Arlidge 1960, McLean 1970).

The subalpine zone occurs throughout the length of the Rocky Mountains primarily as an Engelmann spruce - subalpine fir dominated forest which extends downward about 610 m in elevation below timberline (Daubenmire 1943a). Krajina (1969) characterized the spruce-fir forest as a representative of the Canadian Cordilleran Region and, more specifically, the Canadian Cordilleran Subalpine Forest Zone which appears to be equivalent to Moss' (1953) *Picea - Abies* association of the Cordilleran Forest. Horton (1959) refers to the spruce-fir climax as one of variable pattern according to variation in abundance of the two species *(Picea engelmannii, Abies lasiocarpa)*, and this has created some controversy in characterizing the forest (Bloomberg 1950, Cormack 1953, Beil 1966). Other tree species, including lodgepole pine and black spruce, especially at the lower elevations of the zone, and white-bark pine *(Pinus albicaulis)* on the more exposed ridges, are fairly constant, but minor species of the zone in Jasper and Banff National Parks (Beil 1966).

The structural characteristics of the spruce-fir forest of Jasper and Banff were described as quite variable in understory species, but also quite simple (Beil 1966). Horton (1959) correlated community variation with moisture conditions and noted different growth patterns according to dry, normal and moist habitats.

The spruce-fir forest of the northern part of the province to the S of the study area has been more intensively studied and is often characterized according to habitat types supporting associations. Ogilvie (1962) and Kirby and Ogilvie (1969) designated five major

habitat types for the east slopes of the Rockies near Banff. In Waterton National Park, Kuchar (1973) described several spruce-fir vegetation types for the subalpine area. Several associations appear to be widespread throughout the northern province occurring in N Montana and Idaho as well as southern Alberta (Ogilvie 1962, Kirby & Ogilvie 1969, Daubenmire & Daubenmire 1968, Pfister *et al.* 1974). Subalpine fir appears to be more common than Engelmann spruce S of the international boundary, especially on the W slopes where a number of other coniferous tree species are also important in the zone (Habeck 1967). However, spruce-fir codominance in the interior of British Columbia is quite recognizable as a major component of the zone, though the understory species are quite different than in the Banff and Jasper area (McLean & Holland 1958, Eady 1971). Again studies indicate that some habitat separation of spruce and fir occurs in the mountain ranges closer to the coast, and a monoclimax subalpine fir zone has often been designated (Fonda & Bliss 1969, McLean 1970, Franklin & Dyrness 1973).

As in the montane zone, subalpine communities contain an increasing number of boreal species with increasing latitude (Ogilvie 1962, Moss & Pegg 1963). Subalpine fir extends N into the Yukon Territory to about 64°30'N, but only to about Peace River (55°N) within Alberta (Alexander 1958b).

The spruce-fir forest becomes more open and exhibits a low mat - forming physiognomy (krummholz) at about 2100 m in Jasper (Hrapko 1970). This zone was referred to by Clements (1916) as the "forest-tundra

ecotone" and by Löve (1970) as the "subalpine belt", and has also been described by Billings (1969), quite appropriately, as "ribbon forest". The ecotone has been the subject of several studies in the southern portion of the Alberta Rockies and N Montana. Baig (1972) identified numerous habitat types from north of Banff to the International Boundary, many of which contained subalpine fir or white bark pine as the dominants. The krummholz of Waterton N. P. was characterized by Kuchar (1973) as a scrub of lower elevation conifers (Engelmann spruce, white bark pine, alpine larch) but understory species were often those of the higher tundra communities. Similar findings have been reported for Glacier National Park, Montana, although lower forest understory types were also observed where the spruce-fir scrub was quite dense (Habeck & Choate 1963). The elevation of the tree-line and the expanse of ecotone between forest and tundra is quite variable depending on slope, aspect and topographic geometry (Griggs 1938, Daubenmire 1954, Wardle 1968).

Alpine tundra is the dominant vegetation above this ecotone or belt to snowline which is characterized by a heterogeneity of habitats and communities of low growing perennials (Daubenmire 1943a). Only a few studies have been done on the alpine areas of the Rocky Mountains of Alberta. Moss (1955) discusses the main alpine communities as set forth by Lewis (1917) for the Banff area. Later more intensive work for the Banff and Kananaskis area of Alberta includes that of Beder (1967), Bryant and Scheinberg (1970) and of Trottier (1972). Hrapko (1970) and Kuchar (1975) have made the only intensive studies to date of alpine tundra in Jasper which includes a description of the communities and

environmental parameters which are important in community separation. Hrapko (1970) described fifteen different community-types for Signal Mountain most of which were dominated by dwarf shrubs of *Dryas*, *Cassiope* and *Salix* species. Lichens were found to be a more important part of the flora near snowline at the upper limit of the alpine tundra zone. Kuchar (1975) described a number of communities for the Bald Hills area near Maligne Lake, concentrating on those dominated by *Dryas* spp.

Except for the extensive survey of Kuchar (1973) the alpine vegetation in the southern part of the province has not been studied in detail. Habeck (1967) has described seven major community types for nearby Glacier National Park, Montana, and along with Choate's (1963) more detailed descriptions of the Logan Pass vegetation, contributes most of the information for the area. Cursory attention was given to alpine vegetation by Nimlos and McConnel (1965) on an extensive soil survey of Montana. Bamberg and Major (1968) studied a number of alpine areas further S in Montana and designated correlations between community and soil types. In almost all of the above studies similar community types are described although the composing species may vary. Often descriptions are made on a topographic and/or physiognomic basis and *Carex* and *Dryas* spp. are widespread dominants. Alpine communities in a section of NE British Columbia were dominated by productive *Elymus innovatus*, *Festuca* and *Agropyron subsecundum* types (Brink *et al.* 1972, Lord & Luckhurst 1974). Associated species however, included those traditionally dominant in more southern areas such as *Cassiope*, *Dryas* and *Saxifraga* spp.

B. IMPLICATIONS OF DISTURBANCE

Fires have had the greatest impact upon the vegetation mosaic within the national parks since logging and other post-settlement activities have been limited. Large areas of even-aged lodgepole pine stands occur as a result of widespread fires, which have been curtailed for the most part for the last 50 years with the establishment of the National Parks (Stringer & La Roi 1970). Widespread fires appear to have occurred on a regular basis throughout the northern and far-northern portions of the Rocky Mountains. Larsen (1925) dated large fires in N Idaho for 1870, 1889, 1910 and 1919. Wellner (1970) in an extensive review of fire history also notes the 1910 and 1919 burns for the N Rocky Mountains. Activities associated with railroad construction probably increased the fire frequency in Jasper N. P. (1910-1912, Stringer & La Roi 1970). The extensiveness of lodgepole pine stands throughout the montane zone in Jasper N. P. as well as other areas of Alberta are due to fires during the latter part of the 19th Century (Horton 1956, Smithers 1961).

Studies on the effect of logging in the Alberta Rockies have been primarily directed toward the establishment of economically desirable stands, and have been necessarily conducted outside the national parks. Suitable management practices toward economic logging have been outlined by De Grace (1950) for the area in general. Differences in developmental sequences of S Alberta forests are discussed by Horton (1955) and Day (1972) and recommended management practices have been quite varied. Corns (1972) characterized the regeneration after clearcutting in the

Lower Foothills Section of the Boreal Forest of (Rowe 1959) near Edson and correlated differences with site moisture conditions.

The required conditions for maintaining the desired forest species in E British Columbia have been of interest for a number of years as evident by studies of Barnes (1937), Pogue (1946), Clark *et al.* (1954), Smith (1955), Stettler (1958) and Eis (1967). The requirements for spruce regeneration before and after seed germination has been the main theme of the above studies.

Widespread fires, in addition to promoting the distribution of lodgepole pine, have created large areas of brushland and grassland in Jasper which was conducive to ungulate population increases (Flook 1964). This eventually had a direct effect on the vegetation with many ranges becoming severely overgrazed by the 1940's (Stringer & La Roi 1970). Herd reductions were begun at about this time, and population control policies remain to the present. Although some recovery of the ranges has occurred, evidence of heavy grazing and browsing is still apparent (Stringer & La Roi 1970).

C. SUCCESSIONAL ASPECTS

Intensive investigations into successional sequences after disturbance are quite sparse for the Alberta Rockies, and even more limited for Jasper National Park. Inferences on succession have mostly been secondary to other objectives. Cooper (1916), in a model study, described several seres on moraine in the spruce-fir forest near Mt. Robson. Cormack

(1953) defined several seres for the spruce-fir forests of the S Alberta Rockies following fire and noted that trends and succession rates were variable depending on site conditions. Horton (1955) also recognized sere variation according to site moisture conditions after a 1936 fire in the Kananaskis Forest Experiment Station of the E slopes. Jeffrey *et al.* (1968) recognized the importance of extensive fires during the late 1800s on vegetation types in the upper Old Man River area north of the Crowsnest Pass, and noted that spruce-fir elements were understory components at the time of study.

Sere characterization in the Alberta Rockies has probably been hampered by an active fire suppression policy since the availability of early seral stages are limited to only a few areas. On the other hand, active suppression has allowed for the development of "late successional phases" in a number of areas (Day 1972).

The succession-climax status of dominant conifer species has been of interest in N Idaho and Montana for a number of years. Daubenmire and Daubenmire (1968) identified three developmental or replacement stages for forests after a fire. These include; 1) invasion stage, 2) stagnation stage, and 3) resumption of regeneration. The dominant conifer species of N Idaho were also ranked according to resistance to fire, with *Larix occidentalis* the most resistant and *Picea engelmannii* and *Abies lasiocarpa* among the least resistant. Wellner (1970) in a review of information on fire and succession, summarizes a number of characteristics of conifer species in response to fire. In a similar

area in Montana a complex of conifer dominance was indicated after fires for both the montane and subalpine zones (Habeck 1968). The understory composition of climax communities appears to return relatively quickly after disturbance in these areas, especially when a heavy shrub cover is involved (Daubenmire & Daubenmire 1968). Ericaceous shrubs often appear as diagnostic community components in subclimax lodgepole pine as well as in spruce-fir vegetation (McLean & Holland 1958, Ogilvie 1962, Beil 1966, Hnatiuk 1969).

Variation in the codominance of Engelmann spruce and subalpine fir has initiated some controversy as to subclimax and climax status of the two species (Beil 1966). Self perpetuation success of Engelmann spruce apparently varies with site, and may be as high as subalpine fir or remain higher for a longer period in the eastern vs. the western part of the subalpine forest (Oosting & Reed 1952, Beil 1966, Daubenmire & Daubenmire 1968). Franklin and Mitchell (1967), Daubenmire and Daubenmire (1968) and Day (1972) indicate that subalpine fir may be better adapted to form the climax in the subalpine zone and arrived at similar conclusions from different areas of the Cordillera. Engelmann spruce, because of a longer life-span, still persists as a dominant since most of the forests studied were less than 400 years old. Beil (1966) noted that, although subalpine fir had a higher reproductive potential, Engelmann spruce was still found in all age classes in Banff and Jasper National Parks. He also noted the dynamic character of the spruce-fir climax as indicated by frequent inclusion of lodgepole and black spruce in the lower or more moist area and whitebark pine at higher, more xerophytic exposures along

ridges. Alexander (1974) discusses the current state of knowledge concerning the spruce-fir forests of the western states and notes the importance of a number of environmental factors, including moisture, temperature and light, on regeneration capabilities of both species.

D. INTEGRATED APPROACHES TO VEGETATION STUDY

Although descriptions of plant communities are in themselves useful, the inclusion of quantitative information on causal factors in community composition and distribution adds a needed dimension in ecological understanding. Although most vegetation studies identify one or more controlling factors, the work of Lowdermilk (1925) and Day (1964) on the importance of soil moisture on Engelmann spruce and subalpine fir, and that of Daubenmire (1968b) on community distribution and soil moisture in Idaho, appear especially pertinent to the present study since areas of the Rocky Mountain Cordilleran were involved. Day (1964) also mentions the importance of light intensity as an important factor on tree regeneration and hence stand composition. Another pertinent study includes the early work of Gail (1921) on factors affecting Douglas fir germination and seedling growth.

Recently, studies have become more comprehensive, with more technological sophistication enabling a wider range of environmental measurements, especially those of microclimate. Studies in point include that of Patten (1963) in correlating controlling climatic complexes and vegetation patterns in the Rockies of S Montana, that of Marr (1961) and Langenheim (1962) in the N Central and in E Central part of the Colorado

Rockies respectively, that of Klikoff (1965) for timberline vegetation pattern of the Sierra Nevada of California and the very detailed work of Wolfe *et al.* (1949) on the environmental parameters of a valley in Ohio.

Much of the understanding of climatic-topographic influences on vegetation stems from the work of Geiger (1950). This, along with the integrated approach of the ecosystem concept as discussed by Whittaker (1970), has had an impact on the direction of vegetation, as well as other ecological studies. Ecosystem and natural boundaries such as those of drainage basins or isolated mountain peaks, are often considered identical for study purposes (Whittaker & Neiring 1965, Kirby & Ogilvie 1969). Utilizing the divisive approach to land areas, Rowe (1966) discussed the advantages of using landforms as a common denominator in investigating vegetation and soil types. Pettapiece (1971) utilized a system of landforms and landform complexes in the upper North Saskatchewan River Valley on the eastern edge of Banff park as a major criterion in a soil classification study. It appears logical that knowledge concerning the supporting elements (landforms and soils) of the landscape will enhance the understanding of the vegetation and its component communities as well as other features of the ecosystem.

III. THE VINE CREEK STUDY AREA

A. LOCATION

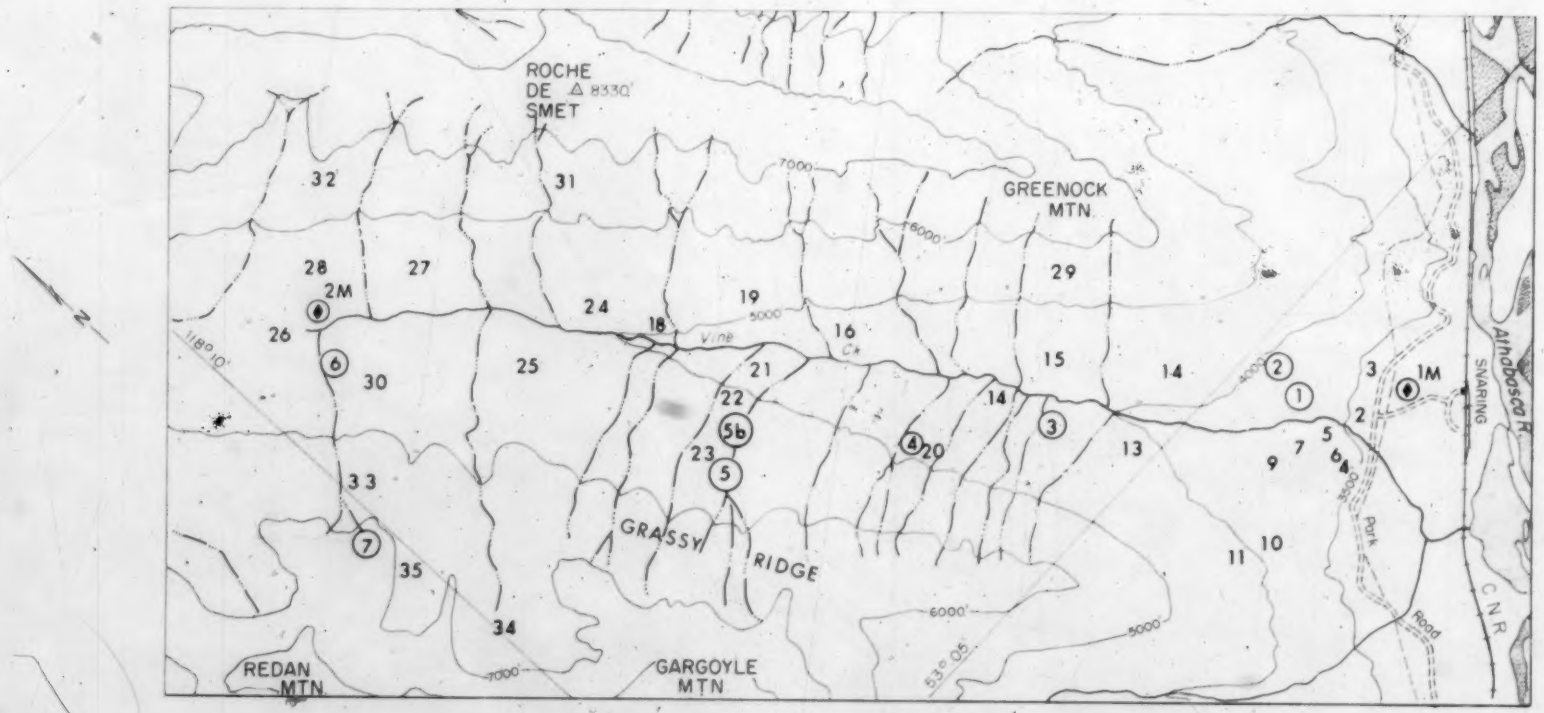
The Vine Creek drainage basin is located 29 km NNW of Jasper, Alberta at 118° 05'W longitude, 53° 05'N latitude and is within the Front Range of the Rocky Mountain complex (Fig. 1). The basin is approximately 10 km long, NW to SE, and 3 km wide, NE to SW, and covers 36 km^2 (slope corrected). Elevation of the headwaters divide at the NW end of the basin is 1700 m (5600 ft) and 1000 m (3300 ft) at the mouth of Vine Creek, the lower end of the basin on the Athabasca River near Jasper Lake. Greenock Mtn (2230 m) and Roche de Smet (2530 m) form the NE boundary, and Gargoyle (2680 m) and Redan Mtns (2590 m) form the SW boundary of the basin.

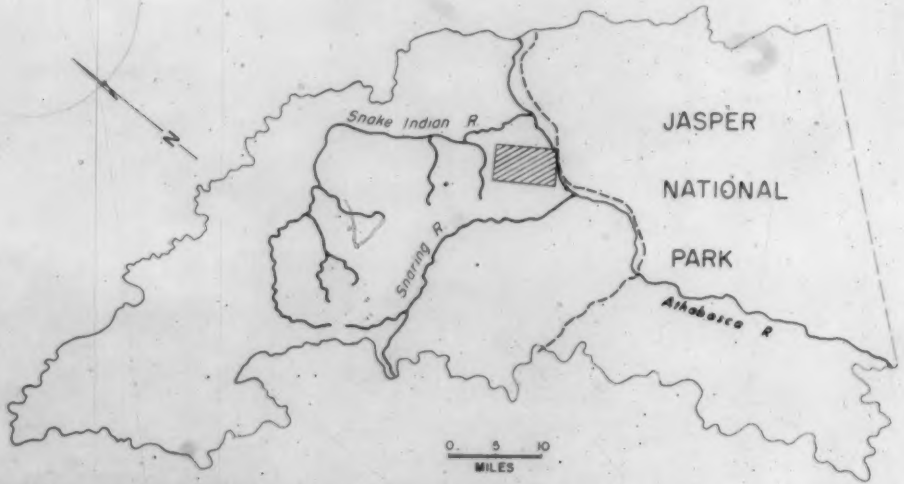
Topography varies from gentle sloping plateaus at the lower extent of the basin to steep cliffs near the ridges. Topographic relief is complex and the valley slopes are dissected by numerous snow and avalanche chutes.

B. GEOLOGY

Geological description follows Brown (1952) and Mountjoy (1962). The Greenock thrust-fault forms the Roche de Smet ridge along the NE boundary of the drainage basin, and the Colin thrust-fault forms the Gargoyle and Redan summit ridge along the SW boundary. The Greenock thrust-fault is homoclinal and contains parallel strata of Upper Cambrian carbonates below discontinuous sub-Devonian strata. Dolomitic limestone

Figure 1. Vine Creek study area, stand and meteorological station locations.





UNCIRCLED NUMBER = STAND

◆ MAIN WEATHER STATION

VEGETATION TYPE WEATHER STATION

(1) PICEA GLAUCA
(2) MONTANE SCRUBLAND
(3) PSEUDOTSUGA MENZIESII
(4) PINUS CONTORTA
(5) PICEA - ABIES / MENZIESIA
(6) PICEA - ABIES / ARNICA
(7) ALPINE TUNDRA

of the Palliser and Sassenach Formations predominate but some calcareous siltstones and breccia are also included. The ridge system along the Gargoyle massif is also mostly of limestone with some siltstone appearing in the Banff, Palliser and Sassenach Formations. Interior to the ridges the dolomitic limestone of the Rundle Group covers a large area and also includes some thin shale beds and light grey organic or partly organic calcarenites. Bedrock between Gargoyle and Redan Mtns also contains yellow-grey and dark grey limestones and calcareous shales of the Sassenach and Mount Hawk Formations. The Palliser dark grey limestone is especially exposed on the Gargoyle headwalls. Reddish sandstone, dolomitic siltstone of the Whitehorse and thin bedded siltstones and silty mudstones of the Sulphur Formations are prominent along the spurs forming Grassy Ridges below Redan Mtn.

Calcareous bedrock forms much of the parent material of the drainage basin either as intact strata near the ridges or as frost shattered rock and colluvium along the valley slopes. Till deposits are also common in the lower portion of the valley and within cirques adjacent to the Gargoyle and Redan headwalls. Alluvium and glacial outwash deposits occur mostly on the valley floor and on the alluvial fan near the Athabasca River where aeolian loess is also quite common. Parent materials are treated in more detail in relation to landform complexes in the Results Section.

C. SOILS

Soil surveys of the mountainous regions of Alberta have been completed in only a few areas. Hnatiuk (1969) described Lithic and Orthic Regosols, Degraded Eutric, Orthic Eutric, and Degraded Dystric Brunisols and Orthic Gray Luvisols for the *Pinus contorta* vegetation of Jasper and Banff National Parks. The soils within the Front Range of the Rockies may have some similarities to taxa described in the comprehensive survey of the Hinton area, but more Regosols are expected in the mountainous terrain (Dumanski *et al.* 1972): Regosols were described as the most prominent type in the montane grasslands of Jasper National Park, but some Brunisols and Chernozems were also identified (Stringer 1973). Jeffrey *et al.* (1968) and Pettapiece (1971) described mostly Regosols within the Front Range along the North Saskatchewan River Valley, but Brunisols and Luvisols were also common. Alpine areas in Banff National Park also contain mostly Regosols although Alpine Eutric Brunisols and Gleysols were described (Knapik *et al.* 1973). Alpine Eutric Brunisols, as well as other Brunisols, occurred frequently under a variety of community types in the Rockies S of Ft. Nelson, B.C. (Lord & Luckhurst 1974).

D. CLIMATE

Long-term meteorological records from Jasper and Entrance, Alberta may be representative of the lower portion of the study area since elevations are similar. However, much of the study area is at considerably higher elevations with different topography and thus different weather patterns are probable. Examination of the long-term reporting

weather station data in the Alberta Rockies indicates that Lake Louise in Banff N.P. may be the most appropriate area for comparison with the upper Vine Creek drainage basin since their precipitation values were similar.

Mean annual maximum and minimum temperature and precipitation normals for the 30-year period 1941-1970 for the three stations are given in Table 1 (Environmental Canada 1970). Devona (Fire Lookout Tower) and Jasper have similar climates, although from the limited data, Jasper appears slightly warmer and drier (Hrapko 1970). Jasper is also warmer and drier than Entrance. The higher elevation of Lake Louise is reflected by a higher precipitation value with more snowfall, and by lower temperatures and number of frost free days (Table 1). Most of the area is affected by the extremes of alternating cold arctic and warm Pacific air masses in winter. Summers may be hot and dry at the lower elevations judging from the near 37°C (100°F) July extreme maximum temperatures and only 40 cm (16 in) mean annual precipitation at Jasper (Table 1).

Table 1. Climatological data[a] from three stations in Alberta most typical to the study area.

Station	Temperature (°C)					No. of frost free days	Precipitation (cm)		
	Mean daily temp.	Mean daily max.	Mean daily min.	Extreme max.	Extreme min.		Annual total	Annual Rain	Annual Snow
Entrance 1006 m, 53°22'N., 117°42'W.	2.2	9.4	-5.0	37.8 (July)	-51.1 (Jan.)	139	51.3	34.8	161.0
Jasper, 1061 m, 52°53'N., 118°04'W.	2.8	8.9	-3.3	36.7 (July)	-46.7 (Jan.)	152	40.13	27.4	137.0
Lake Louise, 1534 m, 51°25'N., 116°10'W.	0.0	7.2	-7.8	34.4 (July)	-52.8 (Jan.)	114	76.7	28.4	481.8

[a]From Canada Dept. of Environment 1970

IV. METHODS

Aerial photographs (1:35,000 ; 1951), including 4 x enlargements, were used to identify and map the major vegetation zones and identify the more obvious landforms. Ground reconnaissance and airphoto interpretation constituted the means for selection of representative stands as well as landform identification and mapping. Each stand had to meet the following criteria before being acceptable for sampling: (1) that it must be a representative sample of a plant community that is common in the basin; (2) that the plant community be physiognomically homogeneous; (3) that the area be at least 200 x 200 m in size in order to minimize edge effects between contiguous communities and (4) that there be no evidence of previous disturbance by man.

A. FIELD SAMPLING

1. Topographic Characteristics and Zootic Influences

The physical setting of each stand within the study area was characterized according to its position in the drainage basin using landform, degree of slope, aspect (^{o}N), and elevation (m ASL). Landform nomenclature initially followed Holmes (1965) and Thornbury (1969), but was later modified according to work more specific to the mountains of western Canada (Pettapiece 1971, Fulton *et al.* 1974), and further air photo interpretation. The degree of slope was measured using a Suunto clinometer and a Thommen altimeter was used for elevation after referencing a known basepoint. Slope aspect was indicated by a compass measurement after correction for magnetic north (26^{o}E declination).

Use by animals was estimated from tracks, trails and browse evidence on vegetation and supplemented with actual sightings. Fire history evidence in the form of charcoal on the ground and on standing trees was noted.

2. Weather Patterns

Air and soil temperature, soil moisture and precipitation data were used to characterize meteorological conditions at certain key points within the drainage basin during the study. Two stations, one at 1040 m and one at 1710 m (Stations 1M & 2M, Fig. 1) were established to monitor weather patterns for the drainage basin. Both stations were located in open areas to minimize the influence of forest cover on the environment. Instruments at these two sites included a Belfort actinograph, a Belfort hygrothermograph, a Moeller distance recording thermograph with sensors at 10, 30 and 60 cm below the ground surface, and a totalizing rain gauge. Temperature recording instruments were housed within a ventilated shelter about 1.3 m above the ground. The actinograph was placed on the shelter's roof. The rain gauges were placed on a stake 1 m above the ground and mineral oil was used to minimize evaporation of collected precipitation.

Major vegetation cover types were used as guides for placement of additional weather stations. Sites were identified on the basis of air photograph interpretation and field reconnaissance in conjunction with stand selection. The vegetation types selected represent the dominant forest and non-forest cover types within the drainage basin, and included:

1) *Picea glauca* forest with *Pinus contorta* and *Pseudotsuga menziesii* 2) montane scrubland - low scrub of *Juniperus communis*, *Calamagrostis purpurascens* and *Arctostaphylos uva-ursi*; 3) *Pseudotsuga menziesii* forest with *Pinus contorta* and some *Picea glauca*; 4) *Pinus contorta* forest with *Picea glauca* x *engelmannii* especially prominent in the understory; 5) *Picea engelmannii - Abies lasiocarpa* forest with *Menziesia glabella*; 6) *Picea engelmannii - Abies lasiocarpa* forest with *Arnica cordifolia* and *Equisetum* spp. and 7) alpine tundra of *Dryas hookeriana*. The stations are numbered according to increasing elevation (Fig. 1).

Instruments at each vegetation site included a sheltered max-min thermometer facing N at 2 m above-ground, Colman soil temperature-moisture blocks at 10, 30 and 60 cm below-ground and a totalizing rain gauge at 1 m height. Shrubs were cleared away from all rain gauges, and mineral oil was added to minimize evaporation.

Each forest type had two air temperature-precipitation stations, one located beneath the tree canopy (not adjacent to tree trunks), and one in a nearby relatively open area. This was done to obtain data on the influence of the canopy on the air temperature and precipitation of the site. In some instances, a non-forest community was used as the comparative site (eg. Station 1M & 1, Fig. 1). The *Picea - Abies/ - Menziesia* type had three stations; forest, open area, and burned area, (5b, Fig. 1), the latter having soil moisture blocks in addition to the thermometer and rain gauge.

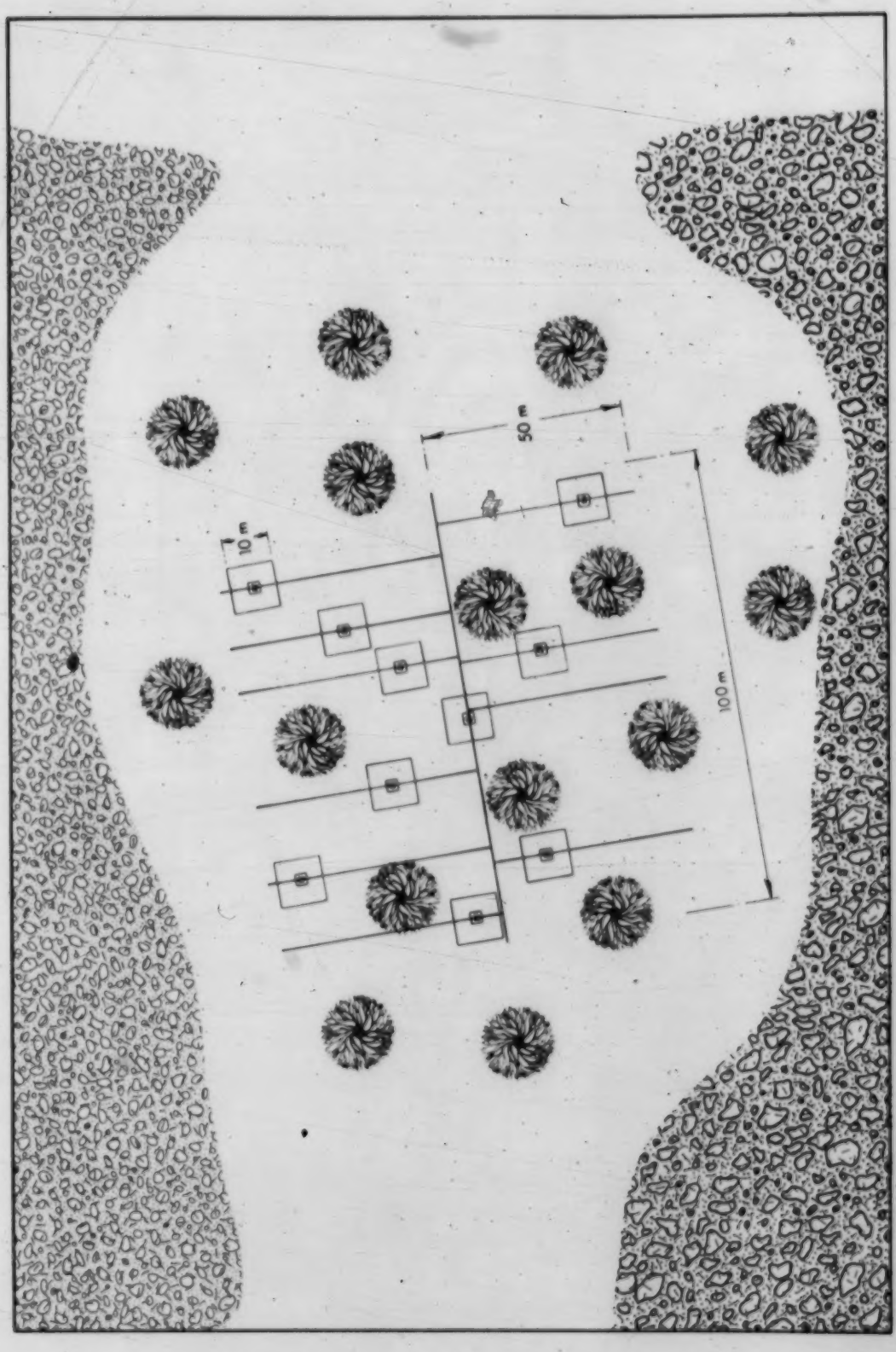
The effect of variable slope exposure were limited somewhat by restricting most of the stations to the NW-NE facing slopes below Gargoyle and Redan Mtns (Fig. 1). Station 2 was an exception facing SW in accordance with the limited distribution of the montane grass scrublands, and station 1 was on a relatively level area.

Data were obtained on a continuous or weekly basis at the two main weather stations, and on a bi-weekly interval at the stations within a vegetation type from June through August of 1970 and 71. The stations closer to the road at the lower end of the drainage basin, and those near the trail along Vine Creek were serviced as often as possible during winter, usually once every month. Equipment malfunction was common due to cold weather, and animals interrupted data accumulation both in winter and summer.

3. Vegetation

A total of 77 potential stands were identified via airphotos, and 35 of these were studied. Each stand was sampled using 10 to 20 nested quadrats which were located from a 100 m baseline along the contour and through the center of the stand. The center of each quadrat was located a random distance (10 to 90 m) along the baseline and a random distance either right (odd) or left (even) 5 to 45 m perpendicular to the baseline. Thus a 1 ha area was potentially available for sampling (Fig. 2). The center of the baseline was permanently marked with a wooden stake containing a numbered metal tag. Twenty quadrats were used in a variety of vegetation types and then tested for adequacy of sampling on a standard

Figure 2. Diagram of sampling scheme using a restricted randomized method of nested quadrat distribution. Sampling in a forested area is depicted.


50 m
10 m
100 m

error to mean tree density ratio (Greig-Smith 1964, p.32), and species-area curve graph. It was felt in the first case that a standard error of < 20% of the mean indicated adequate sampling of the dominant species. Subsequently, a set of 10 nested quadrats was used in the forested areas and 20 quadrats in meadow, low shrub and savanna vegetation.

Structural characteristics of the vegetation were investigated using four main growth-form categories: Tree (> 4 cm dbh), tall shrub (1.5 m ht to 4 cm dbh), herb and low shrub (< 1.5 m ht), and bryoid (bryophytes & lichens). Understory components of the tree species were relegated to seedling (< 31 cm ht), transgressive (> 31 cm ht to < 4 cm dbh) and sapling (4-8 cm dbh) categories for density measurements (stems ha^{-1}).

Ground cover was estimated for each species of the understory using a modified technique of Daubenmire (1959). The following eight cover classes and percent ranges were used: t = < 0.1; 1 = 0.1-1; 2 = 1-5; 3 = 5-25; 4 = 25-50; 5 = 50-75; 6 = 75-95; and 7 = 95-100. Midpoints within these percentage ranges were used in calculating mean cover.

Tree diameter (dbh) and tree and transgressive density for each species, and total standing live and dead were measured within the ten 10 x 10 m quadrats (Fig. 2). Basal area was estimated using a Bitterlich basal area factor 10 measurement for each species from the center of each quadrat. Total canopy cover was obtained by both visual estimates and vertical photographs from the center of each plot according to the

method described in Beil (1966). Mean stand cover was later proportioned according to relative basal area values to obtain a cover percentage for each species, using the assumption that the conifer species have the same potential toward a cover to basal area ratio.

Cores were taken from 10-20 trees of various size classes at 30 cm above-ground on the upslope side to assess stand age structure and relative growth increment. Discs of standing dead and some fallen trees were obtained in burned areas to help date past fires. Heights of cored trees were measured using a Suunto clinometer.

A number of spruce cones (25-70, depending on availability) was collected in appropriate stands for lab analysis of cone characters to produce a morphological character index identifying *Picea glauca*, *P. glauca* x *engelmannii* and *P. engelmannii* populations (see Labratory Methods, p. 36).

Tall shrub, herb and low shrub cover, and tree seedling density were estimated for each species from the nested 2 x 2 m quadrats. Bryophyte and lichen cover was estimated from the 1 x 1 m nested quadrats (Fig. 2). A photograph was taken of each stand.

Voucher specimens of both vascular and non-vascular plants were collected in the 35 stands sampled. A survey of species not occurring in the quadrats was used as a rough measure of sampling adequacy and supplemented species-area curve information. All additional species

were listed on the stand presence data sheets. Nomenclature of vasculars follows Moss (1959), and bryophytes and lichens follow Crum *et al.* (1973), and Hale and Culberson (1970) respectively.

Due to time restrictions, some minor community types were sampled for dominant species on a subjective basis; these included areas too small for the stand sampling scheme and ones with very restricted distribution in the basin.

4. Soils

Two soil pits, one at each end of the baseline, were used to describe and measure the thickness of the soil horizons. Samples were taken from the A, B (when present) and C horizons, air dried and stored, after benzene application to reduce nitrate compositional changes, until laboratory analyses on chemical and physical characteristics could be performed. A reference photograph was taken of one of the soil pits.

B. DATA ANALYSIS

1. Site Characteristics

Continued air photograph interpretation along with field observations were used to classify landform types. Areas of each landform type were calculated using planimeter readings on 4 x enlargements of air photos (1:35,000, 1951 & 1:30,000, 1966).

2. Weather Patterns

Data from thermograph charts of continuous recorded air temperatures were compiled into daily mean and daily mean maximum and minimum values for each month, by using 8 points (every third hour) within each 24 hour period. Maximum and minimum temperatures were used to compare forested and open sites, and sites supporting the different vegetation types.

Air temperature data were also utilized to formulate degree day statistics for the two main meteorological stations (1M and 2M). Degree days were calculated for each month by compiling the mean daily temperature (>0^{o}C) X number of days.

Moisture retention characteristics of each soil sample surrounding each Coleman soil block (10, 30, 60 cm) at each vegetation type station were analyzed by ceramic plate extractions (Richards 1948) and a Soil Test microvolt meter to produce water retention curves and corresponding electro-conductivity (Taylor *et al.* 1961). Saturation, field capacity (-1/3 bar) and permanent wilting point (-15 bars) were utilized to make comparisons of field data from the stations. The curves were then used to plot moisture conditions for the vegetation type stations for the summers of 1970 and 1971 (Stations 1-7, Fig. 1). Soil moisture readings at each site were compensated for variation in temperature and for the calibration coefficient on each Coleman block according to Coleman and Hendricks (1949).

Average solar radiation (langleys day^{-1}) was calculated from actinograph charts on a weekly basis for both main stations using a planimeter (stations 1M and 2M, Fig. 1).

3. Vegetation

Voucher specimens were sorted and identifications were verified by the University of Alberta Herbarium (ALTA), Edmonton, where they are also deposited.

Cone scales of spruce were subjectively analyzed for three characters; 1) stiffness, 2) apex shape and 3) width in relation to distance from the apex, in order to develop a "hybrid index" following Horton (1959) and Beil (1966). Five index categories (0, 100, 200, 300, 400) were used on the basis that 0 = pure *Picea glauca* and 400 = pure *P. engelmannii*. The characters of each cone were ranked into the proper categories, weighted accordingly and summed in order to obtain a mean stand index value (0 - 400).

Mean species cover in each stand was used as the basic data for investigating stand relationships. The population size structure of dominant trees was used to ascertain potential climax species. Agglomerative hierarchical cluster analysis (Pritchard & Anderson 1971) and a two-dimensional ordination (Bray & Curtis 1957) were used as an aid in establishing a vegetation classification. A Fortran IV computer program developed by Conway (1972) facilitated cluster analysis. Ordination was also used for interpreting stand interrelationships and the importance

of a number of biotic and abiotic factors. The technique of Bray and Curtis (1957) was used via a Fortran IV computer program developed by Easton and Precht (no date) which used the equations of Beals (1960) for axis distances and Sorenson's (1948) coefficient of community $\frac{(200\ w)}{a + b}$. The computer program was modified by a number of subroutines to handle large numbers of species (300) (Sparks & Niddrie 1974).

Tree ages were estimated from ring counts on increment cores and discs which were also examined for fire scars. "Effective stand ages" were calculated as the mean of 25% of the oldest trees, after Stringer (1966). An Addo-Ex tree ring counter (courtesy Canadian Forestry Service, Edmonton) was employed to plot growth ring increments of disc and core samples for later use in simple correlation analysis.

4. Soils

Composite soil samples from both pits of each stand were screened for portions < 2 mm which were used in the following analyses. Horizon color was determined using Munsell color charts. Texture was ascertained following the hydrometer method of Bouyoucos (1951) except that samples were slaked in a reciprocal shaker. Both color and textures were helpful in soil classification (Canada Dept. of Agriculture 1970).

Soil samples of 18 stands representing the major community types were analyzed by the Alberta Department of Agriculture, Soil and Feed Testing Laboratory, Edmonton. Analyses were done for NO_3 (after Black 1965), PO_4 (modified technique of Dickman & Bray 1941), K and Na (neutral

1 normal ammonium acetate precipitate), S (turbidimetric method using acetone and acetone extract for optical density), $CaCo_3$ (free lime indication with 10% HC1) and pH (soil paste-glass electrode).

V. RESULTS

The Vine Creek drainage basin was treated as a biophysical unit, i.e. a landscape system of interacting landform, vegetation and soil components. Utilization of landforms provides a stable base on which to relate vegetation and soils units. Landforms also act as integrators of geologic, historic and climatic information (Rowe 1966) and thus are useful land classification criteria (Lacate 1969).

The usefulness of the "plant community" and/or its compositional characteristics as entities for ecological studies has been questioned by Rowe (1966) who emphasized the landform component of the landscape. It is here assumed that the description, identification and mapping of plant communities in a landscape can be undertaken independently, then related to similar knowledge of the compositional, historical and distributional aspects of landforms. It is recognized that landforms are the more stable components of the landscape system and vegetation responds more rapidly to environmental changes. Thus the ultimate need for "integrated studies" is recognized but emphasis on the vegetation component is a valid and useful approach, and within the competence and experience of the author.

A. GEOMORPHOLOGY

Valley formation has conformed to the exposure of two major thrust faults which dip steeply (60-70^{o}) to the SW forming parallel homoclinal ridges (Brown 1952). Both the Gargoyle and Roche de Smet ridges extend

in a NW direction from the Athabasca River Valley (Fig. 1). The Gargoyle ridge on the SW is more complex, having a number of flanks with differing exposures. Glacial evidence is most pronounced high on the N and NE exposed slopes of Gargoyle Mtn, and glaciers were probably a major factor in the formation of the Grassy Ridge complex of subordinate hills. There is little indication of extensive valley glaciation throughout the drainage basin with colluvial deposits the most extensive surface feature and a V-shape exhibited by valley cross-section. Several cirques containing lateral moraines and fossil lake beds formed hanging valleys, but erosional processes since glaciation may have reduced topographic relief (Fig. 1). The saw-toothed ridge of Roche de Smet was probably sharpened by weathering processes of glaciers and snow (nivation) on the N exposures within the Snake Indian River drainage basin. Intact moraines along the lower valley slopes are not readily evident, but till is a common soil feature near the Athabasca River Valley. Glaciofluvial terraces are pronounced only near the lower end of the Roche de Smet and Gargoyle Mtn ridges along the side of the Athabasca River Valley, and are concealed at higher elevations by forest or more often are deformed by subsequent colluvial deposition.

Stream systems are a major topographic feature on both slopes and are the principal erosional force at present. Downcutting through exposed strata is prominent on the Roche de Smet slope, with truncated, twisting stream courses and some waterfalls. The primary creek has smoothed the valley gradient since glaciation with alluvial and colluvial material occurring sometimes below banks of till. A number of colluvial

cones occur near the junction of secondary streams, especially those originating on Roche de Smet. Active snow avalanche chutes are present on both valley slopes, but are more frequent below Grassy Ridge on the NE exposure.

Frost shattering of bedrock, and mass movement processes are apparent in alpine areas. Ridges below Gargoyle Mtn contain solifluction terraces, stone stripes and shattered bedrock outcroppings. Colluvial movement is associated with all of the valley slopes and is evident as loose rock fragments on or near the surface of the soil. Such movement is no doubt accelerated after severe fires. However, most of the valley terrain between avalanche chutes supports well-developed forest vegetation at present and can be regarded as stable.

B. LANDFORMS

Land classification systems utilizing landforms as the basic unit, but recognizing the patterns associated with vegetation, soil and water have been reviewed by Lacate (1969). His land classification system has several hierarchical categories based on the size and homogeneity of an area. The "Land System" is defined as "an area of land throughout which there is a recurring pattern of landforms, soils and vegetation. A rolling, shallow till plain on granite bedrock with yellow birch-balsam poplar forest on Podzolic soils" is given as an example. The "Land Type" category is a smaller unit, and defined as "an area of land, on a particular parent material, having a fairly homogeneous combination of soil (at a level corresponding to the Soil Series) and chronosequence of

vegetation". A well drained portion of a gravelly outwash terrace with an Orthic Dystric Brunisol soil supporting lodgepole pine - *Vaccinium scoparium* vegetation is offered as an example. The "landform" is the fundamental unit and focal point of the Lacate classification, and is defined on the basis of slope and slope patterns, materials that produce relief and origin of the materials when possible. The three-tiered Lacate system is most applicable to terrain of glacial, wind and water origin since a well developed nomenclatural system is in use and most of the landform units are recognizable from air photography. The application of Lacate's classification to mountain land systems is a bit difficult since much of the terrain consists of bedrock or gravity and mass-wasting associated landforms which are less genetic. Alpine areas may be somewhat unique in that nivation and solifluction processes are the principle geomorphic forces shaping the landscape (Russel 1933).

Fulton *et al.* (1974) have developed a landform nomenclatural system applicable to mountain, as well as other types of terrain. The nomenclature is based upon the nature of the landform (consolidated or unconsolidated), the material (genetic categories) and morphology (descriptive adjective). Consolidated bedrock and unconsolidated landform components are treated somewhat differently since not all erosional forces appear in both, but current modifying processes are included in the nomenclature when possible. Thus a basic unconsolidated category such as alluvial veneer could be further qualified for example by "pebbly and eroded" adjectives.

The Vine Creek drainage basin contains a distinctive pattern of relief, geology and associated regional vegetation and therefore is a component unit of the large Land District (composed of several Land Systems) which would also include other drainage basins, especially those with similar geology such as Jacques Creek, located across the Athabasca Valley. Application of the smaller Land System category to the Vine Creek basin presents some difficulties since landforms, vegetation and soils form a very complex mosaic within it. Ridge, valley slope and valley floor "landform complexes" are suggested as three intermediate units for aligning landforms on the basis of highly correlated topographic, geologic and erosional process relationships (Table 2). A similar method was employed by Pettapiece (1971) in using five "Land System" categories, three of which were for areas of the lower slopes. Lithology follows Brown (1952) and Mountjoy (1962).

1. Ridge Complex (I)

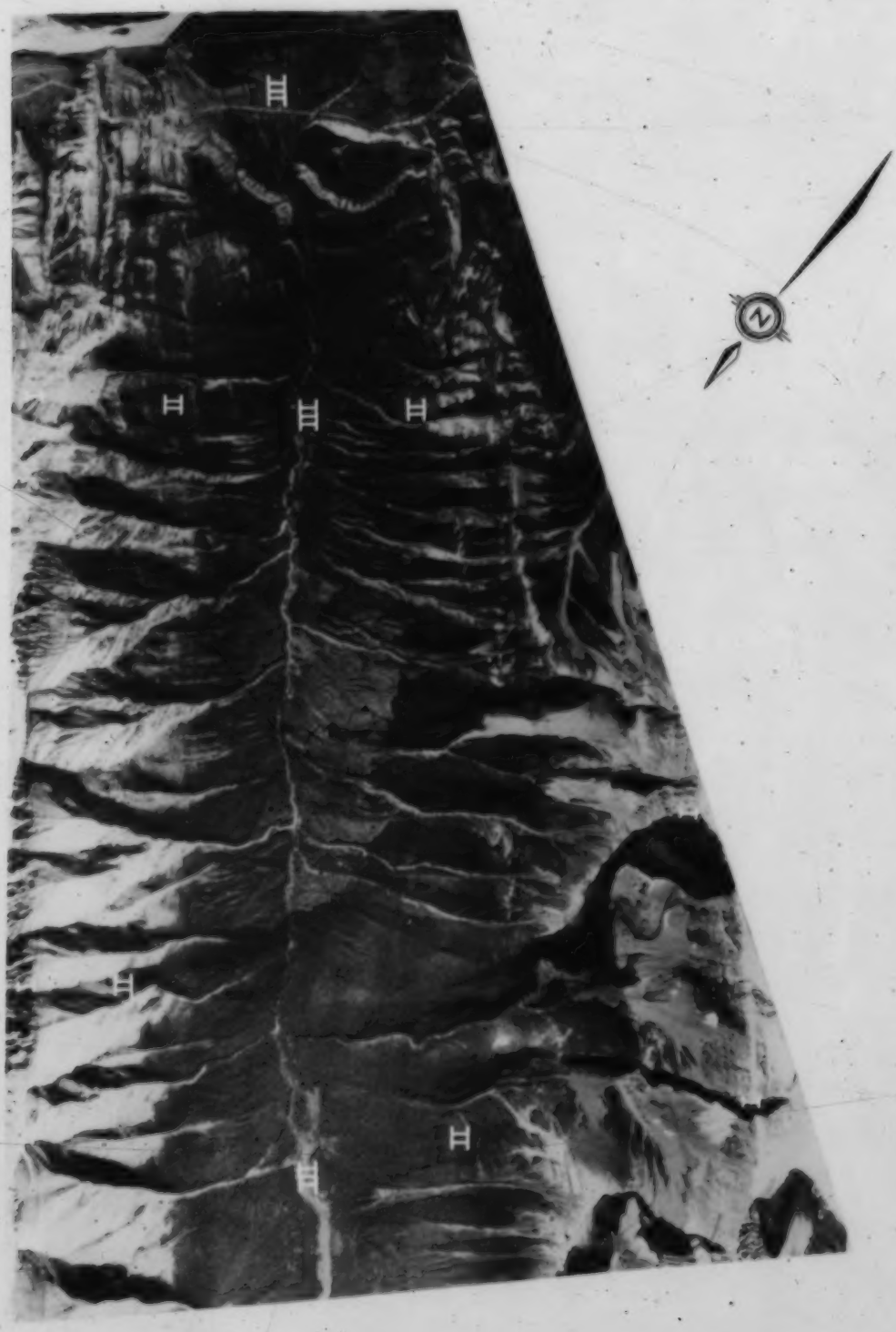
The ridge complex is the simplest, being composed only of bedrock, unconsolidated colluvium and colluvial veneer over carbonate bedrock landform types and comprises 10% of the total drainage basin area (Table 2).

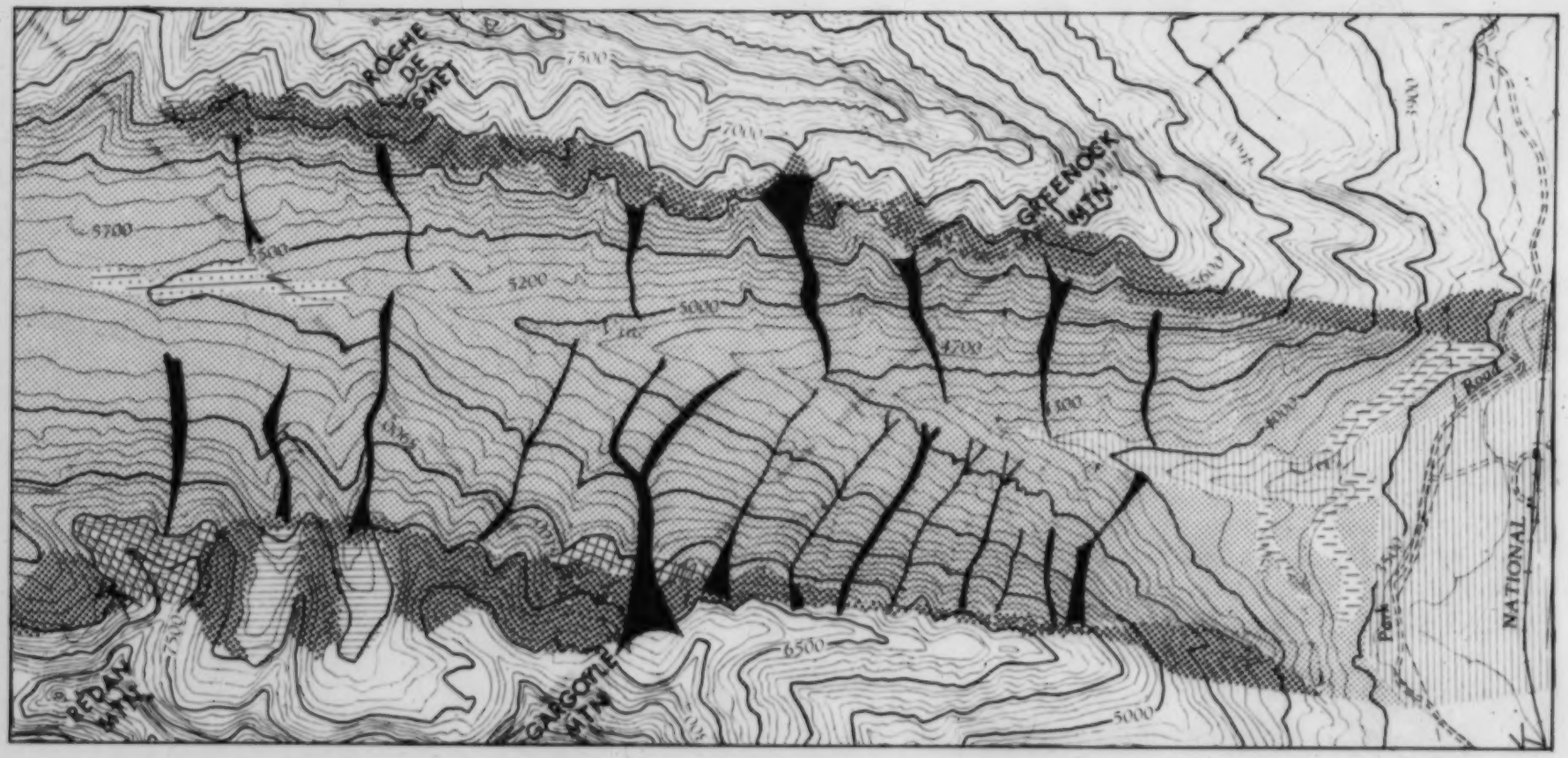
The bedrock of the ridge and headwall of Roche de Smet is formed mainly by the Palliser and Sassenach Formations, with the former dominant throughout the length of the basin. Both are composed mostly of dolomitic limestone, but the yellow-grey Sassenach Formation contains some younger calcareous siltstones and breccia.

Table 2. Landform complexes and landforms of the Vine Creek drainage basin. The abundance of a landform within each complex is indicated as a percent of the total drainage basin area as calculated by planimeter readings from air photography. The landform complex number corresponds to those placed on the air photography (Plate 1).

Landform Complex	Landform	Percent Total Area
(I.) Ridge		10
	Carbonate Bedrock	9
	Unconsolidated Steep Slope (Talus)	<1
	Colluvial Veneer over Bedrock	<1
(II.) Valley Slopes		79
	Carbonate Bedrock	16
	Unconsolidated Steep Slope (Talus)	<1
	Lacustrine Plain (Glacial Cirques)	2
	Ridged Lateral Moraine (Glacial Cirques)	<1
	Constant Colluvial Blanket	49
	Colluvial Blanket and Fan	4
	Avalanche Modified and Gullied Colluvium and Bedrock (Avalanche, Snow and Water Chutes)	8
(III.) Valley Floor		12
	Lacustrine Plain	<1
	Alluvial Terraces	1
	Alluvial Plain (Meander Flood Plain)	<1
	Alluvial Apron (Fan Deposits)	6
	Glaciofluvial Terraces	4

Plate 1. Map of landform distribution within the drainage basin, and airphoto illustrating drainage basin features (1:35,000). The landform complexes are labeled as I (ridge), II (valley slope) and III (valley floor) on the air photograph of the facing page.





LEGEND

I RIDGE II SLOPE

III VALLEY LANDFORM COMPLEXES

2km

Carbonate bedrock

Avalanche and water chutes

Colluvial veneer/bedrock

Alluvial deposits

Glacial cirque (plain w till)

Unconsolidated colluvium

Glaciofluvial terrace

Lacustrine plain

Constant colluvial blanket and fan

The ridges and knolls below the summit cliffs are mostly of the Banff Formation and are predominantly limestone, but beds of calcareous shale and argillaceous organic calcarenite are included. The bedrock has been eroded into a series of hills and nivation cirques or depressions along the length of the ridge, and shale and limestone talus is a common feature (Plate 1). The Banff Formation and dark grey argillaceous limestone of the Palliser Formation are exposed along the eastern flank of the ridge and below Roche de Smet peak at about 1710 m.

The ridge complex formed by the Colin thrust-fault is more complex, having a number of variously oriented spurs (Plate 1). The Gargoyle massif is geologically similar to the Roche de Smet ridge, being comprised mainly of dark grey limestone of the Banff Formation and yellow-grey calcareous siltstone and limestone of the Sassenach Formation. Strata of Grassy Ridge toward the Athabasca River valley are mostly of the Rundle Group of dolomitic limestones but some thin shale beds and light grey organic or partly organic calcarenites are present. The bedrocks between Gargoyle Mtn and Redan Mtn to the west are fairly uniform and are of the Sassenach and Mount Hawk Formation of yellow-grey and dark grey limestone with some embedded siltsone and calcareous shale. The Palliser Formation is exposed on many of the headwalls, especially those associated with cirques near Gargoyle Mtn.

The series of spurs forming the bulk of Grassy Ridge between Gargoyle Mtn and Redan Mtn are mostly of the Whitehorse and Sulphur Formation which are composed of dolomitic siltstone, reddish sandstone and various

limestones in the first case, and dark grey, thin bedded siltstones and silty mudstones in the second. Although bedrock outcroppings are present, much of Grassy Ridge consists of frost shattered material or colluvium with a fairly continuous plant cover. An increase in topographic relief is attributed to nivation erosion between the most resistant strata. Large, windpacked, corniced snowfields are common features along Grassy Ridge and persist through much of the summer.

2. Valley Slope Complex (II)

Steeply dipping and folded carbonate bedrock, unconsolidated steep slopes, lacustrine plain and ridges, lateral moraine (glacial cirques), constant colluvial blanket, constant colluvial blanket and fans, avalanche modified and gullied colluvium and bedrock comprise this landform complex. Valley slopes are the most extensive feature of the drainage basin covering 79% of the total area (Table 2).

Bedrock outcroppings are common on both valley slopes but especially so on Roche de Smet as a series of cliffs which parallel the ridge (Plate 1). Geologically, the cliffs vary from limestone to shale, but the resistant nodular limestone of the Banff Formation and light grey dolomite of the Rundle Group D Formation are most prominent. Banff Formation strata are also exposed below the eastern section of Grassy Ridge. Siltstone and shale inclusions among the limestone are probably responsible here for the light orange coloring which is indicative of weathering (Mountjoy 1962). Other bedrock has been exposed by secondary stream erosion, principally on the steeper Roche de Smet slope. Limestone

of the Rundle Group is again commonly exposed, but inclusions of dark grey siltstone and silty mudstone of the Sulphur Mountain Formation are present below about 1830 m elevation.

Unconsolidated colluvium (talus) on steep slopes occurs mostly above 2075 m near the ridges and headwalls, and as cones at the head of some snow chutes near the ridges (Plate 1). The origin of most talus is limestone, but some red mudstone of the Whitehorse Formation is evident below Redan Mtn. Talus slopes below the de Smet ridge are mostly of grey dolomite, but brown-grey shale is also present. This landform is fairly restricted, covering < 1% of the drainage basin area (Table 2).

The lacustrine plain and ridged lateral moraine are contained within two relatively large glacial cirques below the Redan-Gargoyle ridge at about 1950 m (Plate 1). Lateral moraines form small ridges around the cirque perimeters and limestone block fields and glacial debris are common near the headwalls of Gargoyle Mtn. Both landforms cover only about 2% of the drainage basin (Table 2).

Terminal and lateral moraines other than those in cirques occur along the valley slopes but are usually covered by colluvium. Till material is exposed on some slopes dissected by water courses or avalanche chutes. The influence of the ridge complex on the valley slope complex is less in the lower section of the valley as indicated by intact till deposits which form a system of glaciofluvial knolls and terraces (Plate 1).

The constant colluvial blanket landform is the most extensive comprising 49% of the total basin area (Table 2). It extends from the ridge system to the concave waxing slopes with colluvial fans near the creek (Plate 1). Rock fragments are common on or near the surface of the soil, and some solifluction lobes and rock stripes occur at the higher elevations (ca 2135 m). These higher areas are the more complex portion of the landform with nivated, soliflucted and congeliturbated erosional features being exhibited. The stability of this landform increases toward the valley floor with a deeper soil and less surface debris being exhibited. However, several solifluction slumps occur near the colluvial fan on Gargoyle Mtn and are associated with ground-water discharge from large snowfields. Bedrock beneath the colluvium is mostly carbonate with the Banff, Sulphur Mountain and Whitehorse Formations occurring across most of the slope below Gargoyle Mtn, and the Rundle Group confined to the SE section of Grassy Ridge near the Athabasca River. Similar lithology appears below Roche de Smet, but limestone of the Rundle Group and siltstones and silty mudstones of the Sulphur Mountain Formation are more abundant (Mountjoy 1962).

The colluvial blanket and fan landform occurs nearer the valley floor below the constant slopes, but is discontinuous due to stream undercutting, gullied colluvium deposits and secondary stream channelling. The landform is most abundant in the upper one-half of the drainage basin but composes only 4% of the total area (Table 2). Bedrock of this landform includes strata of the dark to grey shales of the Fernie Formation below about 1400 m. Dolomitic siltstone and sandstones

of the Whitehorse Formation and siltstones of the Sulphur Mountain Formation occur along the upper reaches of the valley floor. Boulders of various origins are commonly exposed within the landform where till deposits have been undercut by the stream. Rock material of diverse origin is a common feature of the landform, since it is affected by both degradation and aggradation processes throughout the basin.

The erosion modified colluvium and bedrock landform is a prominent and dynamic feature of the drainage basin, occurring regularly along both slopes (Plate 1); it covers 8% of the drainage basin area (Table 2). Snow and avalanche chutes are most frequent on the NE slope below Gargoyle Mtn and in the lower one-half of the basin. Most of the chutes on the Roche de Smet slope terminate at the main creek in colluvial fans, whereas many of those from Gargoyle Mtn terminate higher on the slope and drainage into the creek occurs as ground-water with some springs emerging on the slope. The position of the more erodable strata and hence snow fields appear responsible for the position of the chutes and gullies. The reduction of drainage systems directly below the Gargoyle-Redan ridge is due to the influence of cirques drained by single stream systems (Plate 1).

Many of the chutes on Roche de Smet have downcut into bedrock and contain exposed outcroppings and debris, whereas soil development and a vegetation cover is more common on the NE slope of Gargoyle and Redan Mtns. These differences probably result from the initial alignment of the thrust faults and hence strata, erosion of the strata and more till

deposition by glaciers during the Pleistocene on N exposures. Also a more mesic environment with a more gradual release of water from the snowpack, again due to the N exposure of slopes on Gargoyle Mtn is envisioned. Some avalanche chutes below Gargoyle and Redan Mtns were lengthened and widened considerably between 1951 and 1966, according to the airphotos.

3. Valley Floor Complex (III)

The valley floor complex comprises 12% of the total drainage basin area and is confined to a relatively narrow section along the creek. Landforms within it, however, are diverse and include lacustrine plains, alluvial terraces, alluvial plains with cut banks, alluvial aprons and glaciofluvial terraces which extend onto the valley slope (Table 2).

Vine Creek is relatively immature with few meanders and meander plains and has a steep gradient (56 m/km, 295 ft/mi) with rock deposits indicating heavy loads at least during and after intense storms and/or rapid melt and runoff periods.

A lacustrine plain (fossil lake bed) with fine sediments is situated at the head of the valley floor (1710 m; Plate 1). Surface and vadose drainage into the plain from both slopes occurs throughout the summer and headward erosion has occurred toward the lake bed in the vicinity of what appears to be the original outlet. A second lake appears to have occurred near the first at a slightly lower elevation. Modification of

the terrain by slope wash, stream erosion and deposition complicates interpretation of historical features. Moraine is not presently associated with the lake bed and whether it occurred as a result of glacial, colluvial or beaver activity was not determined. Lacustrine plains are also associated with the glaciofluvial terraces in the lower part of the basin and are discussed later.

Alluvial terraces adjacent to the creek are mostly very narrow along the entire length of the valley floor. Several relatively wide terraces occur at about 1130 m (3700 ft) elevation near an alluvial fan (see below). Both high and low terraces occur along much of the creek.

Alluvial plains are closely associated with the low terrace landform, but are formed from point bar deposits. Meander development is not pronounced, although the stream has undercut the slopes in several areas. The lack of well developed meanders is indicative of young streams (Thornbury 1969) and is a common feature of steep mountain watersheds. Collectively the terrace and alluvial flood plain landform cover only about 1% of the total drainage basin area (Table 2).

An alluvial fan commences at about 1130 m elevation and extends to the lowland area near Jasper Lake (1000 m) in the Athabasca River Valley where it coalesces with other fans to form an extensive apron (Plate 1). The landform covers 6% of the drainage basin area (Table 2). The creek is at present confined to the southern portion of the apron and much of the area N of the creek bed is stable, supporting open forest vegetation

with large, rounded boulders commonly exposed. The large size of the fan may indicate a previously more active periglacial deposition period. The apron dissects a large alluvial terrace along the Athabasca River (Jasper Lake) which contains loess that is deposited primarily in winter when numerous point bars are exposed due to low water levels. Alluvial deposits also occur along the creek at secondary stream junctions. Much of the material deposited from secondary streams is composed of coarse rock forming colluvial-alluvial cones, especially below the SW exposed slopes. Further distribution of the material by the main stream has in some instances covered part of the low terrace landform.

Several large Pleistocene glaciofluvial terraces are associated with valley glaciers. Coarse till containing large rocks is exposed along the edge of the terraces which are most apparent on slopes above the major alluvial terraces and apron between 1040 and 1190 m. Lacustrine plains with silty soils occur between some of the knolls and are indicated by a change in community type (Plate 1, p. 46). The alignment of the knolls and terraces suggest that the controlling glacier occurred in the Athabasca Valley. The present creek appears to have cut through the till of the large terrace system, drained the tarns, and produced newer alluvial terraces at various angles to the older material (Plate 1). Terraces and lacustrine plains together cover about 4% of the total drainage basin area (Table 2).

C. CLIMATE

1. General Weather Patterns

Comparisons of temperature and precipitation data from the lower (1040 m; 1M, Fig. 1) and upper (1710 m; 2M, Fig. 1) stations indicate relatively warm, xeric, and cool, mesic environments respectively. Daily temperatures during the three summer months ranged from 0 to 34°C at the lower station, with July 1971 the coolest month, and August 1971 the warmest month (Table 3). The maximum temperature at the upper station was 29°C (July 1970) and the lowest was -8°C (June 1970) during the summer with several months showing a mean daily minimum below freezing (Table 3).

The daily air temperature was about 5°C cooler at the upper station than at the lower station. The mean daily temperature ranges were also greater at the upper (26°C) than at the lower station (23°C). Degree days (> 0°C) varied from 360 to 479 month^{-1} and 125 to 347 month^{-1} for the low and high stations respectively. The difference in climate between the two sites was also indicated by frost frequency with station 1M having, on the average, 0.3 days per month minimum temperatures $\leq$ 0°C, whereas station 2M had an average of 12 days per month $\leq$ 0°C. Of the three summer months, July had the fewest days with temperatures $\leq$ 0°C.

Summer temperature patterns were not consistent for the two years. June was relatively warm in 1970 at both elevations. A wide temperature

Table 3. Summer (June, July and August) meteorological conditions of the drainage basin are characterized by data from stations 1M (1040 m ASL) and 2M (1710 m ASL). Data appears as monthly averages except for precipitation and radiation. Comparisons are made between the study site and the Jasper station (1060 m ASL).

	Air Temperature (^{o}C)			Soil Temperature (^{o}C @ 10 cm)					
STATION	Mean	Max	Min	Mean	Max	Min	Degree Days (> 0^{o}C)	$\bar{x}$ Total Summer Precipitation (cm)	Solar Radiation ($\bar{x}$ ly day^{-1})
1M	14	28	5	31	33	28	432	11.6	579±86
2M	9	23	-3	21	21	20	268	20.4	442±105
JASPER	15	27	6	-	-	-	-	17.3	-

range was exhibited during this month at the upper station (2m) however (Table 3). A warming trend was evident through the summer during 1971.

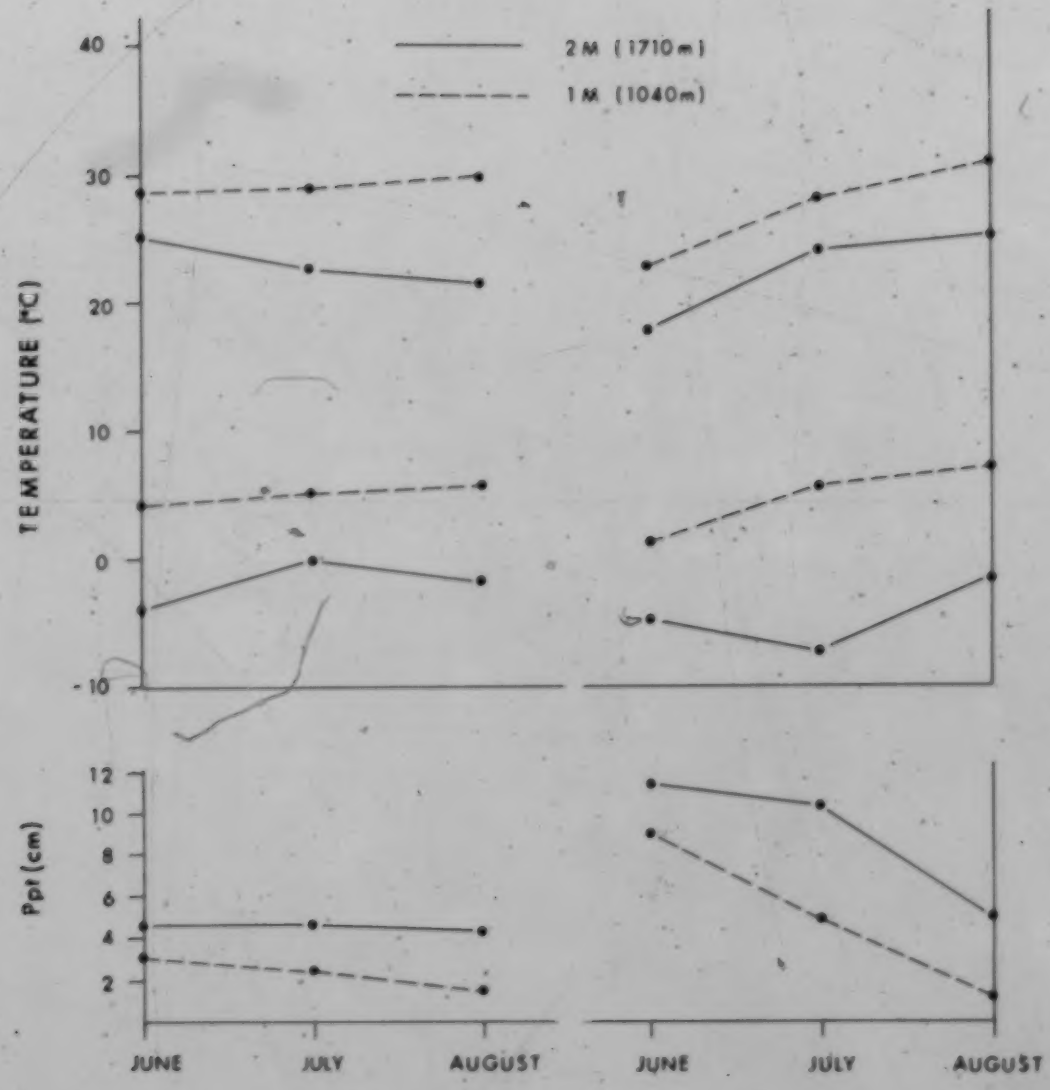
The cooler environment at the higher elevation is also apparent in soil temperature data; monthly maximum and minimum values were 12 and 8°C lower at the upper station (Table 3). The warmest temperatures were at the surface with the lower station having an extreme of 39°C (August 1971), whereas 25°C (July 1970) was the highest at the upper station. Mean monthly maximum and minimum temperatures at 30 and 60 cm below ground were not as extreme.

Mean summer precipitation was 11.6 cm at the lower station and 20.4 cm at the upper, i.e. 1.3 cm 100 m^{-1} elevation increase (Table 3). More precipitation fell in the summer of 1971, and June had the highest amount of precipitation at both stations during that year (Fig. 3).

Average monthly precipitation was 2.8 cm higher at the upper station than the lower station. Differences in amounts were not very consistent, indicating a higher rainfall frequency and the effect of local storms at 1710 m. The highest monthly precipitation total was 11.6 cm at 1710 m (June 1971) and the lowest was 1.6 cm (August 1971) at 1040 m.

Winter conditions were not as well monitored, but similar climatic differentials were indicated between the two sites. The coldest recorded temperature was -47°C, which occurred at 1710 m in January 1971. Minimum temperatures near -40°C were common during both winters at both

Figure 3. Mean monthly maximum and minimum temperatures and monthly precipitation totals for the summers of 1970 and 1971 at the two main weather stations.


2M (1710m)
1M (1040m)
TEMPERATURE (°C)
40
30
20
10
0
-10
Ppt (cm)
12
10
8
6
4
2
JUNE
JULY
AUGUST
JUNE
JULY
AUGUST
1970
1971

elevations. Displacement of Arctic air by warm Pacific air masses (chinooks) was frequent both winters with fluctuations of 8°C hr^{-1} fairly common, and an 18°C increase during a four hour period was the maximum change recorded.

Snow depths in January 1971 were 30 cm at 1040 m and 160 cm at 1710 m. The lower station was often blown or melted free of snow, whereas some snow cover persisted into June at the higher station. Snowfields along the ridges and N exposed cirques and avalanche chutes persisted into August and were augmented by summer snow. Snowfall was observed in every summer month except August, but was usually restricted to the higher elevations. However, an 8 cm snowfall was recorded in July 1971 at 1040 m.

Mean daily total solar radiation averaged 137 ly higher at the lower station (Table 3). Mean reductions from the low to high elevation were 112 and 183 ly day^{-1} for 1970 (excluding August) and 1971. Reduction of solar radiation at the higher elevation was primarily a function of increased cloud cover, and secondarily of shading by the adjacent peaks. Reduction from potential values at 1710 m due to topographic shading by Greenock and Roche de Smet peaks was -70, -45 and -30 ly day^{-1} for June and July of both years, and August 1971, with the variation due to changes in shadow size and duration dependent upon the solar azimuth. Lower daily values were correlated with rainfall periods and cooler air temperatures. Values ranged from 81 ly day^{-1} in June 1971 (1710 m) to 837 ly day^{-1} in August 1970 (1040 m) during the summer months (no data were available during August 1970 at 1710 m).

Comparisons of meteorological data with several other stations illustrate the importance of topography as a controlling factor on local climate. Summer meteorological data at Jasper (1970, 1971) are quite similar to those at station 1M for air temperature (Table 3). More precipitation occurred at Jasper than at station 1M, but less than at 2M (Table 3). The low minimum temperatures at the upper station are a result of nocturnal temperature inversions at the head of the basin and thus a wide max-min range was exhibited.

2. Basin Mesoclimate

Meteorological conditions within the Vine Creek drainage basin are characterized on the basis of summer temperature, precipitation and soil moisture data within the major community types (see Fig. 1, p. 21 for location). The data do not represent the full climatic range of a vegetation zone or habitat type since station replication was not practical.

A number of physical site factors influenced the range of data. Slope and aspect of the sites varied from 2 to 30° and NE to S respectively (Table 4), and are important in terms of the potential amount of insolation available at each station. Elevation, vegetation and edaphic factors also are important determiners of net insolation and the mesoclimate of an area (Oosting 1956, Mowbray & Oosting 1968). Therefore a wide range of mesoclimatic conditions was expected within the drainage basin (Table 4).

Table 4. Physical characteristics of the community type weather stations.

Station	Vegetation Cover Type	Habitat Type*	Elevation (m ASL)	Slope Angle (°)	Slope Aspect	Total Tree Cover (%)	Soil Texture C (% @ 30 cm)	Si	S	Landform
1	*Picea glauca* forest	*Picea glauca/Linnaea borealis/Hylocomium splendens*	1070	2	SSW	35	10	34	56	Alluvial fan
2	Montane scrubland	*Calamagrostis montanensis/ Arctostaphylos uva-ursi*	1090	30	S	-	16	38	46	Glaciofluvial terrace
3	*Pseudotsuga menziesii* forest	*Pseudotsuga menziesii/ Elymus innovatus*	1340	27	ENE	40	19	22	58	Lower constant blanket & fan
4	*Pinus contorta* forest	*Picea/Alnus crispa Elymus innovatus*	1530	22	E	60	16	31	53	Constant colluvial blanket
5	*Picea-Abies* forest	*Picea engelmannii-Abies lasiocarpa/Menziesia glabella-Vaccinium membranaceum*	1740	18	NE	55	14	46	40	Constant colluvial blanket
5b	*Pinus contorta* forest	subclimax of above	1710	12	NE	40	20	23	57	Constant colluvial blanket
6	*Picea-Abies* forest	*Picea engelmannii-Abies lasiocarpa/Arnica cordifolia*	1740	10	ENE	75	16	32	52	Constant colluvial blanket
7	Alpine tundra	*Dryas hookeriana-Oxytropis podocarpa*	2015	25	NE	-	7	42	51	Colluvial veneer over bedrock

* Climax Associations.

2.1 Maximum - Minimum Air Temperatures

Both the highest (32°C) and lowest (-4°C) summer temperatures occurred in August 1971 at the elevational extremes of the stations (1 and 7 respectively, Table 4). A summer warming trend was evident for stations 1 through 5, but maximum and minimum temperatures were lower in August at stations above about 1700 m (station 5b, Table 5).

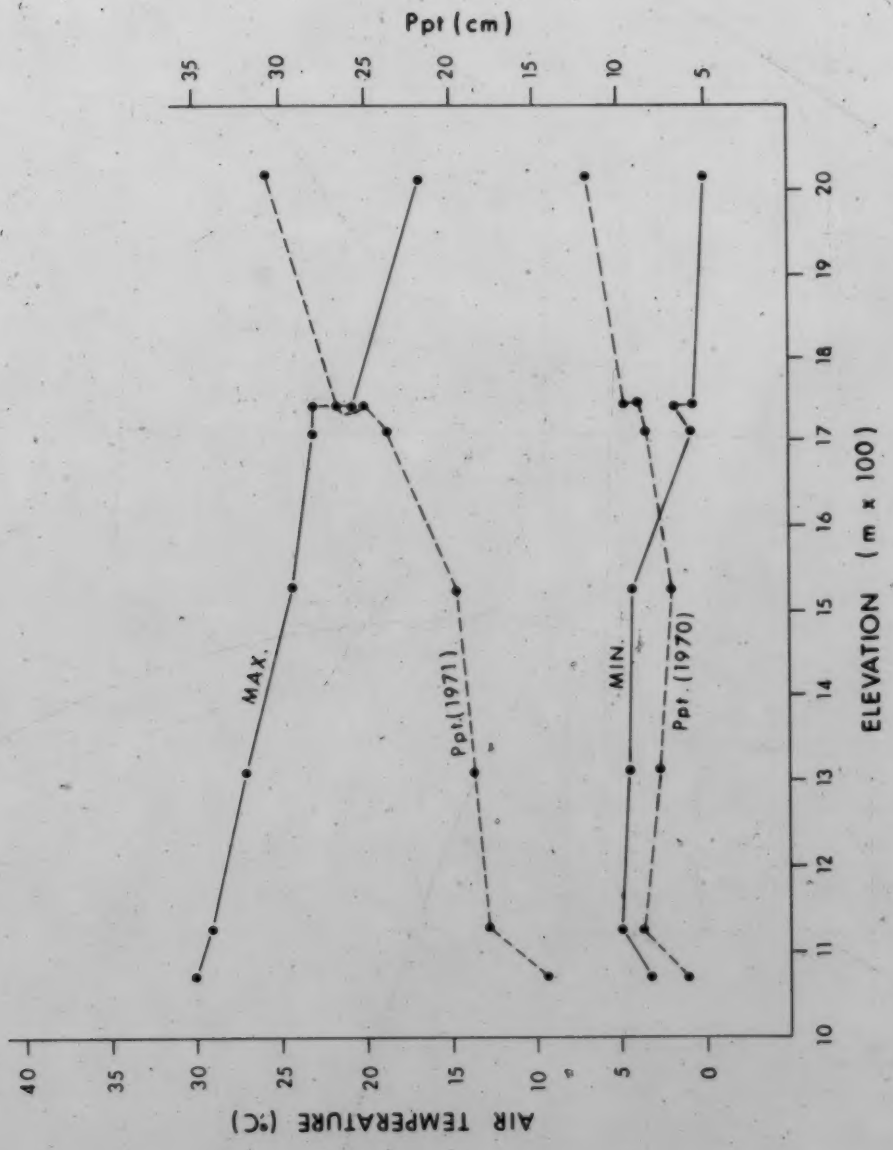
A range of 20 to 25°C was common between station maximum and minimum temperatures, with differences of 29°C (station 2, August 1971) and 14°C (station 7, July 1970) the recorded extremes in range (Fig. 4). The wider ranges occurred at sites located at the base of the constant colluvial blanketed slopes and are probably in response to cold air drainage. Thus temperature ranges are often wider at stations 1 and 6 than those at the respective upslope stations 2 and 7 (Table 5).

A temperature decrease along the elevation gradient was apparent throughout the study period with average differences of 12 and 5°C between station 1 and 7 for maximum and minimum values respectively. The correlation was significant for both maximum ($r = -0.94$, $p < 0.01$) and minimum ($r = -0.84$, $p < 0.01$) values with expected reductions of 1.1 and 0.4°C 100 m^{-1} elevation increase respectively. The temperature gradient was steepest in August 1970 for maximum values, and in August 1971 for minimum values, and is due to an upper level cooling trend near the end of August (station 7, Table 5).

Table 5. Monthly maximum and minimum summer air temperatures (°C) at the community type weather stations. Values are a mean of two readings.

Station	1970						1971						$\bar{X}$ Total	
	June		July		August		June		July		August			
	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min
1	29	5	29	3	31	6	26	1	29	1	33	4	30	3
2	30	5	29	6	31	5	25	2	28	3	32	8	29	5
3	28	7	26	9	27	5	23	1	28	3	27	7	27	4
4	-	-	26	6	26	4	18	1	25	3	25	6	24	4
5	-	-	28	4	22	2	16	0	23	0	25	4	23	2
5b	-	-	24	2	24	1	17	-2	25	0	23	3	23	1
6	-	-	23	4	21	2	16	-4	23	0	23	4	21	1
7	-	-	17	3	17	-1	13	-4	19	0	19	0	17	0

Figure 4. Change in air temperature (mean summer maximum and minimum) and total summer precipitation for 1970 and 1971 with change in elevation. Generally, a cooler, moister environment is indicated with elevation increase.


Ppt (cm)
35
30
25
20
15
10
5
MAX.
Ppt.(1971)
MIN.
Ppt. (1970)
AIR TEMPERATURE (°C)
40
35
30
25
20
15
10
5
0
ELEVATION (m x 100)
10
11
12
13
14
15
16
17
18
19
20

2.2 Precipitation

Summer precipitation increased significantly with elevation, 2 cm 100 m^{-1} ($r = +0.94$, $p < 0.01$), with station 7 having about twice as much as station 1 (Table 6). The fact that most of the stations (1, 3, 4, 5, 5a, 6) were beneath a forest canopy complicates interpretations (see below), but precipitation differences between paired stations (beneath the canopy and open) were not consistent enough to change the expected precipitation/elevation relationship (paired t-test). The higher storm frequency at the head of the valley is evident as a sharp precipitation increase at 1740 m (station 2M; Fig. 4).

The summer precipitation pattern was reversed for the two years with about 41% falling in August during 1970 and 47% falling in June during the summer of 1971 (Fig. 4). Both June and July of 1971 had a much greater amount of precipitation than any other summer month, and stations in 1971 had more than twice the amount of rainfall that was recorded in 1970 (Table 6). Monthly summer precipitation varied from 1.6 cm for August 1971 at station 4 to 13.5 cm in June 1971 at station 7.

2.3 Forest Canopy Influence

Comparisons of temperature and precipitation data of paired stations indicate a trend toward a wider temperature range and a greater amount of precipitation in open areas. In two instances data from the main weather stations are used for comparisons since they were located close to community-type stations (i.e., station 1 vs. 1M and station 6 vs. 2M).

Table 6. Monthly precipitation totals (cm) of the community type stations for the summers of 1970 and 1971.

Year	Month	Station and Elevation (m) 1 1070	2 1130	3 1310	4 1530	5 1740	5b 1710	6 1740	7 2015	Monthly Total
1970	June	2.1	2.4	1.8	2.4[1]	2.4[1]	2.4[1]	2,4	3.2	19.1
	July	2.0	2.4	1.9	2.9	3.1	2.2	3.3	3.6	21.4
	August	2.3	3.7	3.9	2.1	3.4	3.8[1]	3.9	5.3	28.4
	Total	6.4	8.5	7.6	7.4	8.9	8.4	9.6	12.1	
1971	June	8.4	10.3	9.0	9.3	10.5	10.9[1]	11.0	13.5	82.9
	July	3.6	4.8	6.40[1]	8.9	12.0	10.1[1]	10.0	12.3	68.1
	August	2.8	2.5	2.8[1]	1.6	2.5	2.5	5.7	5.8	26.2
	Total	14.8	17.6	18.2	19.8	25.0	23.5	26.7	31.6	

[1]Missing data calculated by plotting regression equations from field values.

Stations beneath a forest canopy received an average of 2.2 (1970) and 3.6 cm (1971) less precipitation per summer than those in open areas (Table 7). Total summer reductions of precipitation beneath the canopy varied from 0.4 cm at station 3 in 1970 to 4.4 cm at station 6 in 1971. A 3.1 cm reduction occurred at station 4, the highest for a single month.

Although measured summer precipitation was 25 and 26% higher in open area stations 4 and 6, no consistent differences occurred for all stations (paired t-test, $p < 0.10$). Interception of precipitation was low at stations having a canopy cover < 41% (1, 3 and 5B), and high at those with a relatively dense canopy (Table 7).

The canopy had a greater effect on maximum than on minimum temperature values; and a significant difference was observed within the 1971 maximum data (paired t-test, $p < 0.10$). Minimum values in the open area at the head of the drainage basin (station 6) were quite marked in response to cold air drainage.

2.4 Soil Moisture

The water potentials of 0, -1/3 and -15 bars are used as threshold values for plotting the soil moisture conditions of the eight sites. It is realized that -1/3 bars (field capacity) and -15 bars (permanent wilting percentage) are more meaningful in relation to agricultural crop species than as critical thresholds for most species in natural systems. Possible errors due to drying and wetting of the soil during electro-

Table 7. Magnitude and direction of change of precipitation (cm total month^{-1}) and monthly maximum and minimum air temperature (°C) from beneath the forest canopy to near-by open areas at five locations within the drainage basin. Positive values would be expected for precipitation and maximum temperature, and a minus value for minimums with no tree canopy interception of rain and wider temperature extremes in the open areas. Dots indicate not enough data for a comparison.

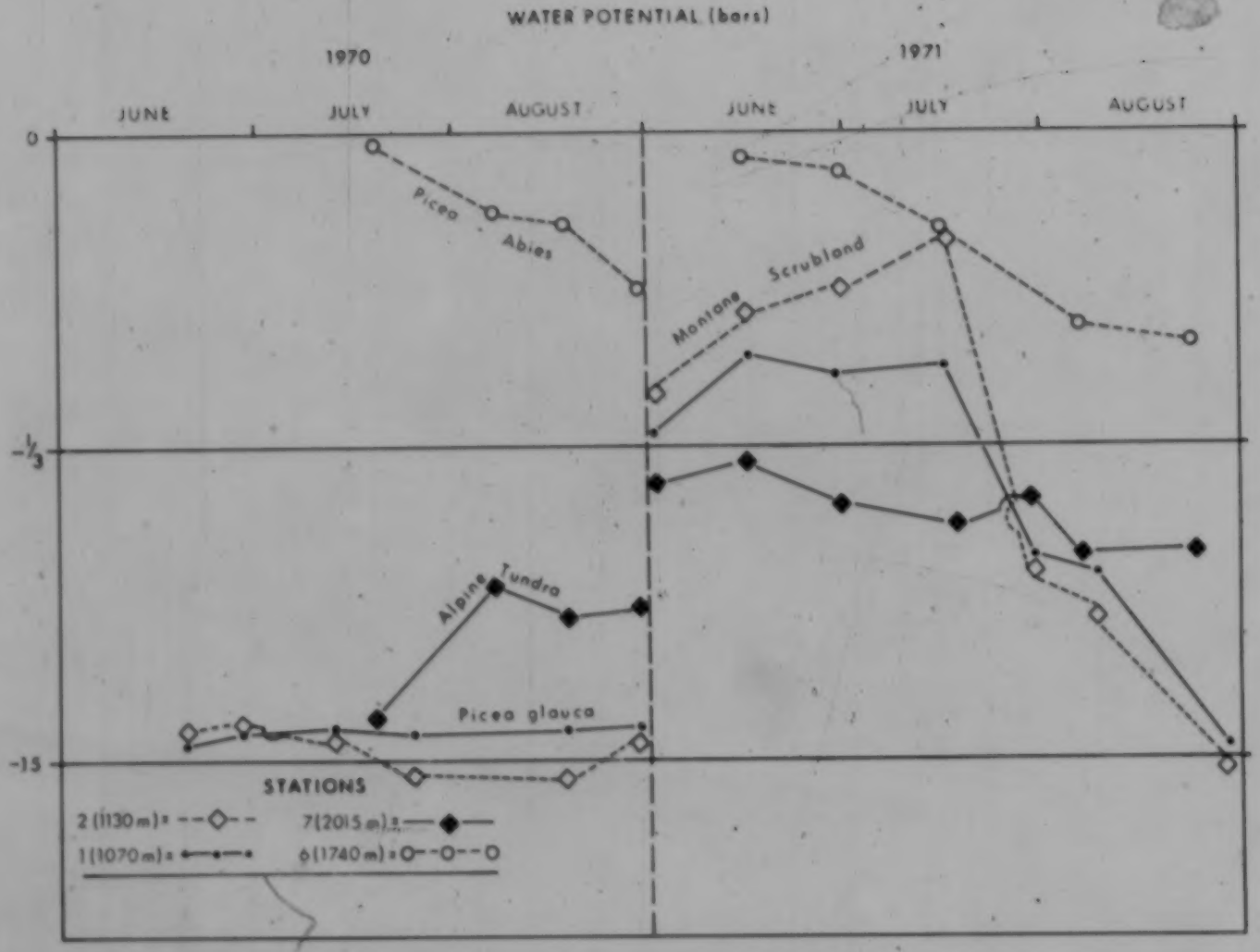
Year & Month		Parameter	STATIONS 1	3	4	5b	6
		Ppt.	+1.2	-0.1	.	.	+2.1
	June	Max.	-1	+2	.	.	.
		Min.	-1	0	.	.	.
		Ppt.	+0.4	0.0	+0.9	+0.2	+1.1
1970	July	Max.	-1	+2	-2	+2	0
		Min.	-2	-1	-2	0	-4
		Ppt.	-0.5	+0.3	+1.6	+0.4	+0.4
	August	Max.	-1	+2	0	+1	+1
		Min.	0	-1	0	-1	-4
$\bar{x}$ Monthly		Ppt.	+0.4	0.0	+0.8	+0.3	+1.2
difference		Max.	-1	+2	-1	+1.5	+0.5
		Min.	-1	-0.5	-1	-0.5	-4
		Ppt.	+0.9	+0.1	+2.5	.	+1.6
	June	Max.	-3	-1	+1	+2	+2
		Min.	+1	0	-1	0	0
		Ppt.	+1.2	.	+3.1	.	+2.5
1971	July	Max.	-2	+1	+1	+1	0
		Min.	-5	0	-2	0	-6
		Ppt.	+1.2	.	.	+2.2	+0.3
	August	Max.	-2	0	+2	+3	+3
		Min.	+3	0	-3	-1	-5
$\bar{x}$ Monthly		Ppt.	+1.1	+0.1	+2.8	+2.2	+1.5
difference		Max.	-2.5	0	+1.3	+2.0	+1.7
		Min.	-0.3	0	-2.0	0	-3.7

conductivity calibration and the nature of point readings preclude using the data to determine absolute soil moisture regimes. Rather the data are used on a comparative basis to help characterize the drainage basin mesoclimate in relation to season, elevation and topographic setting.

Water potentials at 10 cm depth were more variable than those at 30 or 60 cm, and showed a quicker response to precipitation and return to dry conditions. Values more negative than -15 bars were common at 10 cm while near 1/3 bar values were simultaneously present at lower depths. Potentials at 60 cm were usually similar to those at 30 cm, but remained high in response to recharge by percolation or run-off. Many stations had near zero water potentials at 60 cm in June and July 1971, and none had potentials more negative than -15 bars during the entire study period at this depth. Water potentials at 30 cm are used to compare the soil moisture regimes of the stations since a majority of the roots were found within this depth while placing the moisture blocks.

Station soils below 1710 m became progressively drier from June to August of 1970 with potentials mostly between -1/3 and -15 bars, and then became slightly more moist through August in response to an increase in precipitation (Fig. 5). Stations above 1710 m showed different trends with *Picea-Abies* stations (5 and 6) exhibiting moist soils, but having a drying trend through August. The alpine station (7) on the other hand exhibited an increase in soil moisture, but this remained well below the -1/3 bar water potential (Fig. 5).

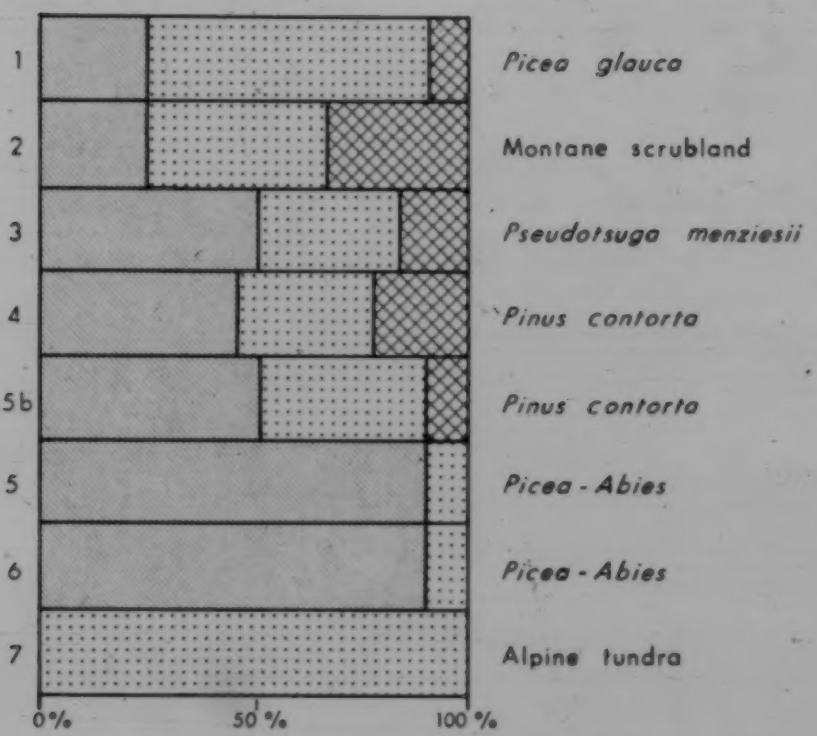
Figure 5. Seasonal change in soil moisture at 30 cm depth at the *Picea glauca* (1), montane scrubland (2), *Picea-Abies* (6) and alpine tundra (7) weather stations. The stations included had the most extreme soil moisture conditions.


WATER POTENTIAL (bars)
1970
1971
JUNE
JULY
AUGUST
JUNE
JULY
AUGUST
0
-⅓
-15
Picea
Abies
Montane
Scrubland
Alpine Tundra
Picea glauca
STATIONS
2 (1130 m)
7 (2015 m)
1 (1070 m)
6 (1740 m)

Soil moisture conditions were much more striking during 1971 with a seasonal march from wet to dry soil regimes exhibited for most stations. All sites maintained water potentials less negative than -1/3 bars through the first part of July in 1971, but this was succeeded by a rapid drying period in August, especially at the lower elevations with some water potentials more negative than -15 bars (Fig. 5). Stations 1, 4 and 5, although exhibiting a drying trend in late summer, had potentials within the -1/3 to -15 bars range. Higher elevation sites 5, 6 and 7 had less of a seasonal gradient, with most potentials remaining near -1/3 bar (potentials of station 6 and 7 are shown in Fig. 5).

The most xeric soil regime occurred at station 2 (montane scrubland) where 30% of the readings, including one in September of 1971, were more negative than -15 bars (Fig. 6). Station 3 *(Pseudotsuga menziesii)* and 4 *(Pinus contorta)* were quite similar with 16 and 20% of the observations more negative than -15 bars. Uniformly moist conditions were displayed at stations 5 and 6 with 90% of the water potentials less negative than -1/3 bar. The burned portion of the *Picea-Abies* vegetation (5b) exhibited a more xeric soil regime than that in the unburned area (5) with values more negative than -15 bars in August 1970 and early September 1971. Soil moisture at the alpine tundra site (station 7) was maintained between -1/3 and -15 bars even though the area had the greatest amount of precipitation. The site was well drained, however, with a relatively steep slope (25°) and coarse shale substratum (soil textures are given in Table 4).

Figure 6. Distribution of soil moisture readings at 30 cm depth during summer months of 1970 and 1971. Stations are ranked according to increase in elevation (1070 to 2015 m).



WEATHER STATION

< - 15 BARS

-1/3 TO -15 BARS

0 TO -1/3 BARS

The soil water potentials can be used for ranking the eight sites along an environmental gradient using the information in Figure 6. However, it is difficult to make comparisons since a number of combinations are possible using the three ranges of water potentials. Therefore an index scale is proposed as a method of judging the relationship among sites. Indices were calculated using 5, 3, 1 for coefficients of < -15, -15 to -1/3 and > -1/3 bars water potentials respectively. The percentage of observations for each station were multiplied by the coefficient and summed. The index potentially could range from 500 for a very dry site to 100 for one with near zero water potentials. The ranking of indices on Table 8 gives the following order of stations on a xeric to mesic gradient; Montane scrubland (2), Alpine tundra (7), *Picea glauca* (1), *Pseudotsuga menziesii* (3), *Pinus contorta* (burned *Picea - Abies* h.t.; 5b), *Pinus contorta (Picea - Alnus* h.t.; 4), and *Picea - Abies* (5 & 6). The index values indicate that the moisture regimes of stations 1, 3, 4 and 5b are quite similar and tend to follow the elevation gradient. Station 4 *(Picea - Alnus)* reflects a mesic environment, occurring on a N exposure and having a closed canopy. Station 5b appears slightly drier having a more open tree canopy. Soil moisture on the steeper slopes (stations 2, 7) was lowered by rapid runoff and seepage loss after rains. The combination of a steep slope (30^{o}), warm aspect and open physiognomy produced the most xeric soil regime (montane scrubland, station 2; Fig. 1). The alpine tundra site, although having relatively large amounts of precipitation, had a very rocky substrate with little mineral soil which no doubt decreased the soil moisture content. Stations 5, 5b, 6 *(Picea - Abies)* and 3 *(Pseudotsuga menziesii)* were affected by

Table 8. Soil moisture indices for the eight community type stations. Potential indices range from 100 to 500 on a mesic to more xeric gradient. The stations were numbered according to increasing elevations, and ranked from driest to wettest according to index values.

Vegetation Cover Type	Station	Water Potential (Bars) Frequency % 0 to -1/3 (1)	-1/3 to -15 (3)	< -15 (5)	Index
Montane scrubland	2	25	135	150	310
Alpine tundra	7	0	300	0	300
Picea glauca	1	25	189	40	254
Pseudotsuga menziesii	3	50	102	80	232
Pinus contorta	5b	50	120	50	220
Pinus contorta	4	45	60	100	205
Picea - Abies	5	90	30	-	120
Picea - Abies	6	90	30	-	120

ground inputs from higher areas. Stations within *Picea - Abies* forest (5b, 5, 6) were below snow fields which were present most of the summer.

Station 1 *(Picea glauca)* acted as a discharge basin at the base of a glaciofluvial terrace containing the Montane scrubland, and thus less negative water potentials would be expected in comparison to the higher site. However, a higher boulder and soil sand fraction at station 1 probably caused the soil moisture potential to be more negative, especially during dry periods; thus the comparable value to station 2 during portions of the growing season (Fig. 5). A steeper slope and warmer exposure probably account for the more negative potentials at station 4 cf. 3 since their soil textures are similar and precipitation was greater at the upper site (Tables 4 and 6).

It is concluded that moister mesoclimates along the gradient in Figure 6 are due mainly to lower temperatures and greater amounts of precipitation, but that a number of other factors including slope steepness, exposure, topographical position, soil texture and compaction, and community physiognomy are important in producing the soil moisture regime.

D. VEGETATION

1. Flora and Presence

A total of 285 vascular, 26 moss, 6 liverwort and 32 lichen species and subspecies of 73 families were identified within the Vine Creek basin. Of these, 254 taxa were observed within the 35 stands of vegetation selected for this study. A number of species were widely distributed. Those having stand presence > 60% included *Elymus innovatus*, *Linnaea borealis americana*, *Pinus contorta latifolia*, *Hylocomium splendens*, and *Pleurozium schreberi*. *Rosa acicularis*, *Fragaria virginiana*, *Galium boreale*, *Juniperus communis*, *Shepherdia canadensis*, *Pyrola secunda*, *Cornus canadensis* and *Arnica cordifolia* had stand presences of $\geq$ 50%. Seventy species were observed in only one stand (presence of 3%); many of these occurred in stands at the elevational extremes of the basin. A complete list of species is given in Appendix 1.

2. Species Richness of Stands

The mean number of species per stand was 33, and varied from 24 in a white spruce forest at the lower part of the valley (stand 1) to 53 in a subalpine meadow within a glacial cirque (stand 35). However, no significant trend appeared between species richness and elevation ($r = +0.37$, $p < 0.05$). The *Pinus contorta* forest generally contained more species than those of *Pseudotsuga menziesii*, *Picea glauca* or *Picea engelmannii - Abies lasiocarpa*, and may reflect the influence of fire on the habitats. Species richness was not significantly correlated with canopy cover ($r = +0.15$).

3. Zonation

About 80% of the basin had a continuous vegetation cover (Table 9). Forest was the predominant structural type, extending from the mouth of the basin to about 2100 m elevation (ASL) and characterizing the montane and subalpine zones; the latter were most readily recognized by changes in the forest types. Scrub and meadow types comprised only a minor percentage of the total vegetation and were distributed throughout the larger forest matrix. Elevational limits of the major zones were often difficult to delineate precisely and in the montane were somewhat arbitrary due to topographic irregularity. Fires have increased the vegetational complexity and the lower elevational boundary of the *Picea engelmannii - Abies lasiocarpa* forest is dominated at present by *Pinus contorta*.

3.1 Montane Zone

The montane zone was typified by mostly mixed forests of *Picea glauca, Pseudotsuga menziesii* and *Pinus contorta* between 1000 and about 1600 m (Table 9). The only pure stands were formed by *Picea glauca* on terraces at the mouth of the creek on Jasper Lake. *Pinus contorta* was more common in the montane zone but has extended upward in elevation after fire. A combination of fire and topographic aspect has permitted *P. contorta* and *Pseudotsuga menziesii* to reach 1800 m on steep S-facing slopes.

Montane grassland and scrubland occurred most extensively between 1060 and 1160 m on S-facing slopes of glaciofluvial terraces and on

Table 9. Major vegetation zones, their elevations and approximate percent of total area. Percentages were obtained by planimeter measurements and 1:8,750 aerial photographs. Elevational range includes the area where zonal vegetation types are best developed as recognized in the field and on aerial photographs, with overlap representing different aspects.

Vegetation Zone	Percentage of Total Area	Elevation (m)
Montane	32	1000-1600
Forest	92	
Grassland	8	
Montane-Subalpine Transition	12	1400-1700
Subalpine	33	1600-2100
Forest	89	
Meadow & Scrub	11	
Alpine	23	2100-2300
Vascular Tundra	17	
Rock & Lichen Tundra	83	

portions of the alluvial fans which were slightly elevated above the stream channels. Characteristic floristic elements of these structural groups included *Juniperus communis*, *Shepherdia canadensis*, *Rosa acicularis*, *Arctostaphylos uva-ursi*, *Antennaria* spp. and a number of graminoid species. These extended to about 1800 m, but were confined to the steeper S-facing sections of avalanche chutes and hence constitute a small portion of the total area (Table 9).

3.2 Montane - Subalpine Transition

Mixtures of montane and subalpine species form a transition zone which covered a relatively large portion of the forested area (Table 9). The mixing of elements characteristic of either zone is in response to topography, with subalpine elements extending into N-facing swales or frost pockets, and conversely, montane elements more abundant on steep S-facing areas. The presence of a morphologically "intermediate" spruce *(Picea glauca x engelmannii)* may typify the transition between montane and subalpine forests and is discussed in a later section.

3.3 Subalpine Zone

The subalpine zone was typified by *Picea engelmannii* and *Abies lasiocarpa* co-dominated forest which extends from about 1560 m to 2040 m on NW and to 2190 on SE exposures respectively, along Grassy Ridge below Gargoyle and Redan Mtns. This forest extends to about 1980 m on the rocky S exposed slopes of Roche de Smet. The transition from forest to meadow or low shrub vegetation was fairly complex and is affected by slope steepness and aspect. Krummholz (twisted, matted

conifer scrub) of *Picea engelmannii*, *Abies lasiocarpa* and *Pinus albicaulis* was common at treeline on N exposures but occurred disjunctly on the rocky S-facing slopes of Roche de Smet where outlying spires of *Picea engelmannii* and *Pinus albicaulis* (to 4 m ht.) were more common, especially below and adjacent to rock outcrops. Treeline extended about 150 m higher in elevation on SE than on NW exposures on Grassy Ridge (Plate 1, p. 46). Comparisons of treeline on the two major valley slopes were difficult since much of the Roche de Smet area is of steep exposed rock faces and a distinct climatic tree-line is not realized. Soil formation has occurred only on the more moderate slopes and hence the vegetation was disjunct.

Subalpine meadows were most extensive near the upper limit of forest at about 2070 m, but were scattered throughout the zone in N-facing avalanche chutes and also at the head of the valley in a fossil tarn. A number of subalpine and alpine species (*Valeriana sitchensis*, *Phyllodoce empetriformis*, *Arnica diversifolia*) also formed the understory of krummholz and upper subalpine forest vegetation. The subalpine meadow vegetation was confined primarily to glacial cirques and snow or avalanche chutes, and it comprised only about 4% of the total study area (Table 9).

3.4 Alpine Zone

Only 20% of the total area above tree-line (23% of total basin area) contained continuous vegetative cover with the balance occurring as rock and lichen tundra (Table 9). Alpine tundra, typified by *Dryas*

hookeriana dominance, was confined primarily to the rounded slopes of Grassy Ridge between about 2100 and 2300 m elevation. Below this, heath (*Cassiope* & *Phyllodoce* spp.) and meadow (*Poa alpina*, *Carex* & *Luzula* spp.) communities extended into krummholz and the upper forest, especially on N-facing slopes.

Rock and lichen tundra types occurred to the elevational limits of the peaks with *Saxifraga oppositifolia* and *Trisetum spicatum* occurring disjunctly to about 2350 m on N and on S exposures 2450 m but becoming more confined to rock crevices containing soil at the higher elevations. Lichens (*Cetraria nivalis*, *C. pinastri*, *Stereocaulon tomentosum*, *Thamnolia* spp., *Parmelia* spp.) were quite abundant at the upper elevational limit of the study area.

4. Morphological Gradation between *Picea engelmannii* and *P. glauca*

Problems in the identification of *Picea glauca* and *P. engelmannii* led to the use of a morphological index (MI) based on cone scale characters. Index values ranged from 0 (pure *P. glauca*) to 400 (pure *P. engelmannii*) and follow Horton (1959). Details on methods and results are given in Appendix 6. "Intermediate spruce" was designated, for purposes of identification and data analysis, as those having MI values between 100 and 300 (Table 10). However, a morphological gradient was indicated by the index, and in fact pure populations with no intermediate contamination are apparently rare in the mountain region of Alberta (Horton 1959, Beil 1966). The correlation between MI values and elevation was significant ($r = +0.86$, $p < 0.01$), but the largest mean MI did not occur at the highest elevation (Table 10).

Table 10. Mean morphological index (MI) values based on conve scale apex shape, width and stifness.* *Picea glauca* = 0-100, Intermediate = 100-300, *P. engelmannii* = 300-400.

Stand	Elevation (m)	Exposure	Angle (degrees)	Mean MI	MI Range in Stand
1	1000	0	0	24	0-100
2	1050	NE	3	63	0-200
4	1075	WSW	2	38	0-100
5	1130	SE	3	57	0-200
7	1150	WSW	6	89	0-200
10	1280	E	29	52	0-200
11	1300	ESE	15	59	0-200
13	1330	ESE	15	59	0-200
14	1360	E	9	92	0-200
17	1470	SW	20	137	0-200
18	1495	S	7	245	0-400
19	1530	SW	23	242	0-400
20	1570	E	27	251	0-400
21	1600	NE	18	289	0-400
22	1610	NE	19	260	0-400
23	1615	WSW	19	284	100-400
24	1615	SW	10	307	100-400
25	1635	W	9	313	200-400
27	1680	SSW	11	312	100-400
28	1720	SSW	6	378	300-400
29	1740	SW	30	261	0-400
30	1770	NE	15	326	200-400
31	1840	SW	28	326	100-300
32	1900	SW	33	218	200-400
33	2040	NE	33	336	200-400

* after Horton (1959)

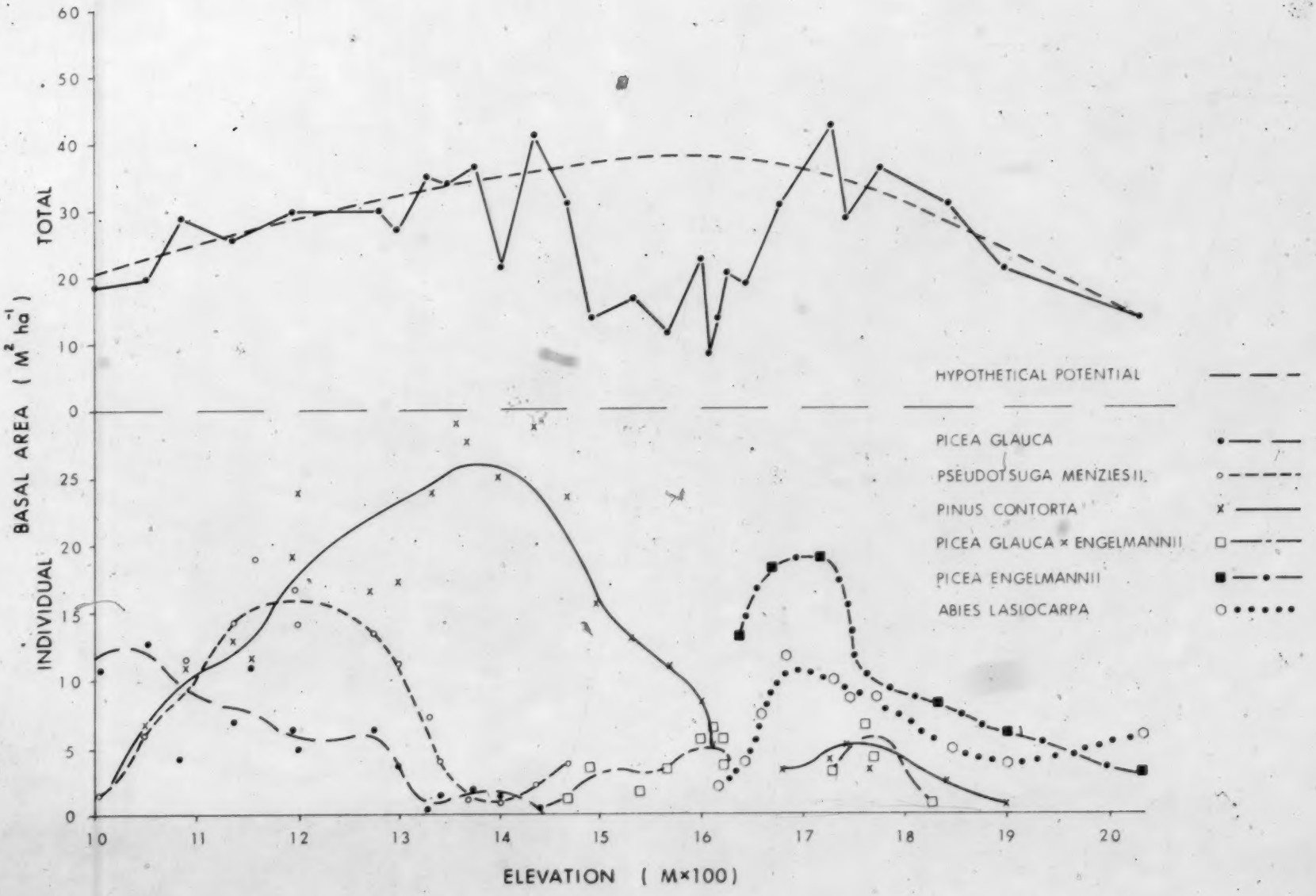
Picea populations in nine stands were regarded as *P. glauca;* these stands ranged from the base of the valley to about 1450 m. "Intermediate spruce" *(P. glauca* x *engelmannii)* populations were identified primarily between 1360 and 1620 m, but stands 29 and 32 on steep S exposures at still higher elevations contained MI values below 300 (Table 10). Populations of seven stands were rated as *P. engelmannii,* but introgression from *P. glauca* was still evident, especially near the 1600 m contour. Higher MI values occurred on the more level sections of the S-facing slope (stand 28) and at the higher elevations on N-facing slopes (stand 33; Table 10).

5. Distribution and Abundance of Tree Taxa

The seven dominant conifer trees, *Picea glauca, P. glauca* x *engelmannii, P. engelmannii, Pseudotsuga menziesii, Pinus contorta, P. albicaulis* and *Abies lasiocarpa* show definite elevational correlations and occur differentially through the basin. Less important tree species included *Picea mariana, Populus balsamifera, P. tremuloides* and *Betula papyrifera. Acer glabrum douglasii, Alnus tenuifolia* and *A. crispa* appeared within the tree canopy in some stands, but were more often classed as tall shrubs.

The distributional pattern exhibited by the dominant tree taxa, though controlled primarily by factors associated with elevation, also varied as a result of different slope exposure and steepness and fire history. The distribution and abundance of the major tree taxa are shown by plotting estimates of their basal area (m^2 ha^{-1}) along an elevational gradient (Fig. 7).

Figure 7. The distribution of basal area of six conifer species along an elevation gradient of the drainage basin. Line irregularity in the individual and total estimates is due to variation in fire history and topography. A hypothetical basal area is given in which variance in these and other factors is essentially eliminated.


BASAL AREA (M² ha⁻¹)
TOTAL
INDIVIDUAL
ELEVATION (M×100)
HYPOTHETICAL POTENTIAL
PICEA GLAUCA
PSEUDOTSUGA MENZIESII
PINUS CONTORTA
PICEA GLAUCA × ENGELMANNII
PICEA ENGELMANNII
ABIES LASIOCARPA

The "harmonization" technique of Douglas (1936) and Curtis and McIntosh (1951) was utilized to smooth the data into more normal curves and to obtain an idea of the basal area potential by reducing the impact of topographic variability and elevation discontinuity. The average was computed using the formula; $(a + 2b + c)/4$, where a, b & c are successive observations.

Picea glauca basal area was relatively low except in mature stands that have been fire free for about 200 years. Such communities occurred predominantly on alluvial terraces at about 1000 m and in sheltered coves between glaciofluvial terraces to about 1150 m on the N-facing valley slope (Fig. 7).

Pseudotsuga menziesii was also an important component of the cove forests. It occurred, however, more dominantly in forests on steeper and more southerly exposed slopes between about 1100 and 1300 m, most of which also exhibited evidence of fire. Thus the basal areas of both *P. menziesii* and *P. glauca* were below their potentials, and especially in the case of the former, exhibited relatively high values below 1300 m because of pre-fire relicts (Fig. 7).

A major portion of the burned area of the basin is now represented by extensive *Pinus contorta* stands, with corresponding high basal area values. Although the last burn (ca 1910) extended to about 1600 m, *P. contorta* did not establish as readily at these elevations, especially on NE-facing slopes.

"Intermediate spruce" and *Abies lasiocarpa* increased in dominance from about 1560 m which marks the beginning of the subalpine zone (Fig. 7). As with *P. contorta*, the present distribution and abundance of intermediate spruce and *A. lasiocarpa* reflects the extent of the last fire as abrupt basal area curves at about 1600 m elevation (Fig. 7).

Maximum basal area values of *Picea engelmannii* occurred between 1700 and 1800 m on the lower valley slopes near the head of the basin. A decrease in *P. engelmannii* and an increase in *A. lasiocarpa* basal area occurred thereafter with increasing elevation (Fig. 7) and is especially evident on the N-facing valley slope. Both species had decreasing basal areas at elevations above 1800 m.

Disjunct populations of "intermediate" spruce and *Pinus contorta* appeared as the major components of high S-facing or ridge-top forests between 1740 and 1840 m above the subalpine spruce-fir vegetation (Fig. 7). *Pinus albicaulis* occurred in these stands but only in one case (stand 32) did it approach a basal area of $5 m^2 ha^{-1}$.

An indication of total forest growth patterns was obtained by plotting the total basal area against elevation (Fig. 7). Irregularity in the line is attributed to a combination of fire history and topographic variation of stands. Areas on steep, S-facing slopes usually contained lower basal area values which were accentuated by a relatively recent fire history. Again, the burned area at the lower section of the subalpine forest occurred as a series of relatively low values between

1450 and about 1650 m. This is postulated as reflecting the reduced ability of *P. contorta* to assume an aggressive successional role after fire in the subalpine zone, and rather, shrubs appeared to become more important along the elevation gradient. The fire-induced reduction of the forest biomass is emphasized by plotting a hypothetical potential on which topographic and fire history variability are essentially eliminated (Fig. 7).

Populus tremuloides and *Betula papyrifera* occurred mainly as minor components of the montane forest vegetation below about 1400 m and never exceeded basal areas of 2 m^2 ha^{-1}. *P. tremuloides* was most abundant in a small stand below a slope-washed area with a SE aspect. *Picea mariana* was generally present between 1400 and 1770 m in wet areas within the spruce-fir forests, but usually had a basal area of less than 1 m^2 ha^{-1}.

6. Classification of Communities

6.1 Classification Criteria

The "association" of Daubenmire (1952, 1968a) was used as the basic plant community classification unit. He defines the association as "all climax stands in which the dominants of corresponding layers are essentially the same, to the extent that any differences in composition are due to chance dissemination or to a transitory historic factor rather than to a fundamental dissimilarity in habitat potentialities". An association represents a particular "habitat type" that supports stands of similar plant communities. Daubenmire (1968a) noted that much of the landscape is presently in a subclimax state, and thus information on the potential

climax community is usually derived from observations on seedlings of known climax or shade tolerant tree species and from a number of known climax understory species which regenerate relatively quickly following disturbance. In the event that disturbance is severe enough that a seral community is long-lasting the term "associes" was suggested. The association is named by the most important species of the constituent "unions" (synusiae) which are normally separated by a diagonal line (Daubenmire & Daubenmire 1968). The association concept listed above is in contrast to the "community types" of Whittaker (1967) and Langenheim (1962) which are more empirical, though successional gradients between types are recognized in studies using this concept. The habitat type is postulated as giving more information on the potential of the land and thus more useful in land-use planning.

The association habitat types (h.t.) of the basin were grouped into "Series", following Daubenmire and Daubenmire (1968) which resemble elevationally defined vegetation zones. Topographic and edaphic influences reduce the usefulness of adhering strictly to a zonal, i.e., elevational approach, however. The problem became most evident during the process of relegating *Pinus contorta* dominated stands to either *Picea glauca* and "intermediate spruce" or *Pseudotsuga menziesii* h.t.s.

Density statistics within seedling, transgressive and sapling size classes were used to ascertain self-reproducing tree species populations, and hence initial aggregation of forested stands into a Series (Appendix 2). Problem stands appeared within montane *Pinus contorta* dominated

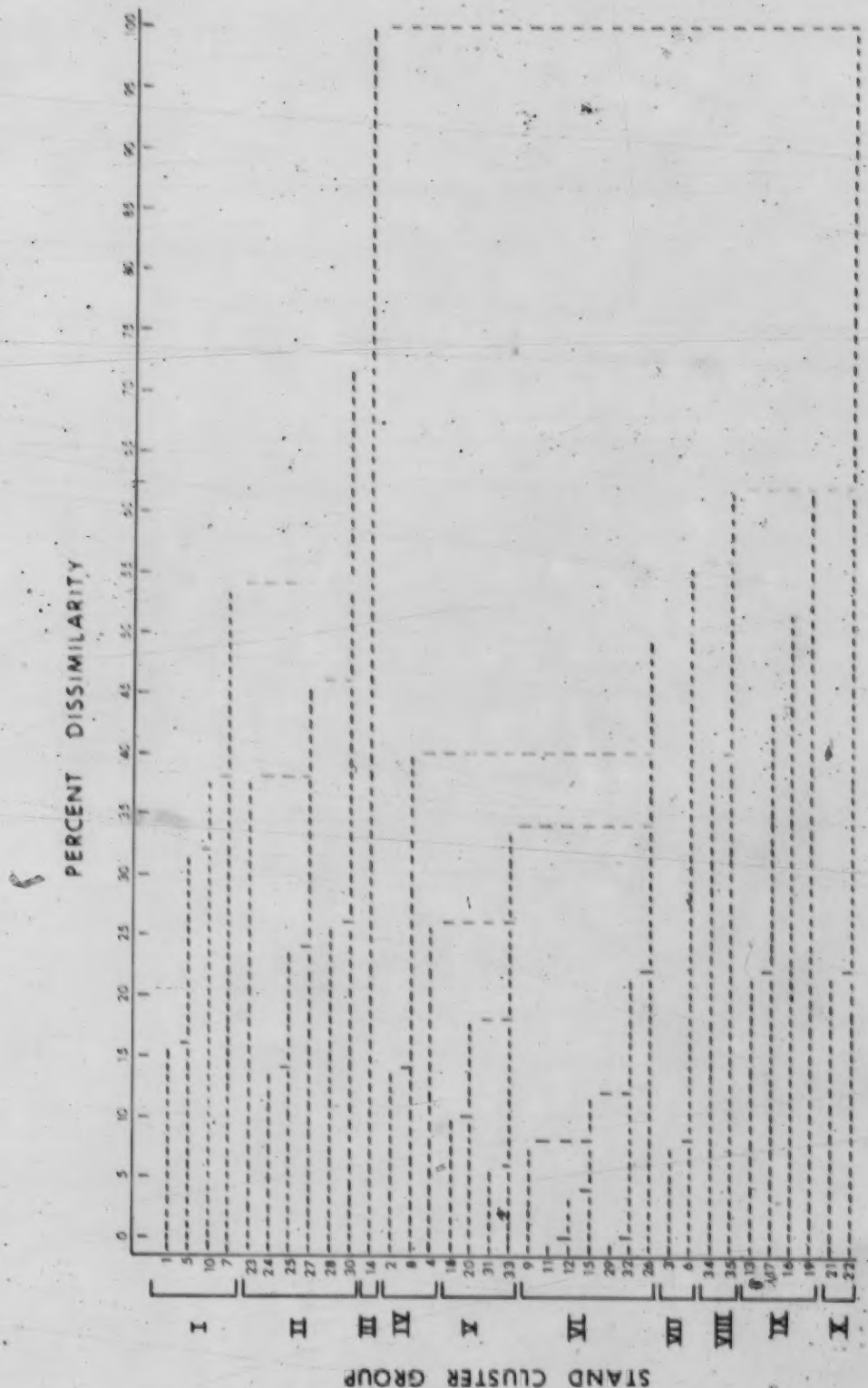
areas of the forest with *Pseudotsuga* and *Picea* seedlings sometimes occurring in nearly equal quantities (see Appendix 2). In these cases the floristic composition was eventually used to ascertain an affinity to a more easily defined association, and thus Series. *Picea engelmannii* (including "intermediate" spruce) and *Abies lasiocarpa* were treated as climax codominants of the Subalpine Forest Series. The climax status of *P. engelmannii* apparently varies according to location (Daubenmire 1952, Oosting & Reed 1952, Krajina 1969), but it appears to be a self-maintaining population along with *Abies lasiocarpa* in much of Jasper N.P. (Beil 1966).

6.2 Cluster Analysis and Ordination

Numerical techniques of both agglomerative hierarchical cluster analysis (Pritchard & Anderson 1971) and ordination (Bray & Curtis 1957) using the Sorenson (1948) coefficient of community to calculate a stand similarity index, were employed to assess inter-stand relationships. A similarity matrix is given in Appendix 3.

Three cluster analysis dendrograms using different methods (Furthest Neighbor, Group Average and Minimum Variance) for calculating inter-cluster distances gave quite similar stand groupings. Similar findings were reported by Pritchard & Anderson (1971) and Achuff (1974). The dendrogram of the Furthest Neighbor cluster appeared to contain the fewest unrelated single stand groups and is given in Figure 8.

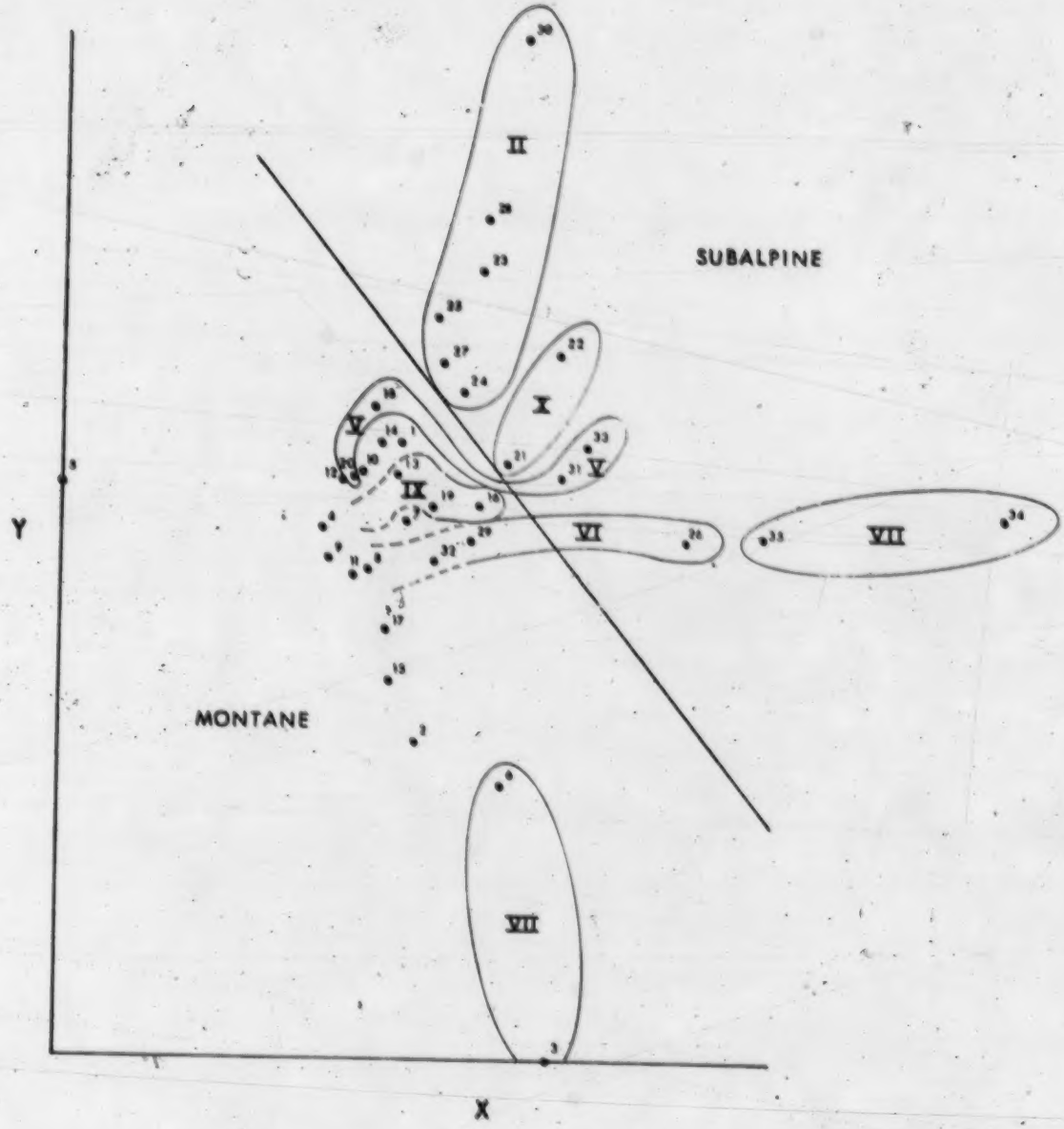
Figure 8. Agglomerative hierarchical cluster analysis of the 35 stands. Ten relatively distinct clusters were recognized, with most of these segregated beyond the 20% level of dissimilarity using the Furthest Neighbor method of distance calculations.


PERCENT DISSIMILARITY
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100
I
II
III
IV
V
VI
VII
VIII
IX
X
STAND CLUSTER GROUP

Ten rather distinctive clusters were recognized from the dendrogram; most were amalgamated with other clusters beyond the 20% point of the dissimilarity scale (Fig. 8). Two large groups (stands 1-14 and 2-22) were immediately evident and reflect the abundance of *Hylocomium splendens* and/or *Pleurozium schreberi*, and an increase in *Juniperus communis* as well as increased stand heterogeneity, respectively. Combinations of abundant but fairly ubiquitous species including *Elymus innovatus*, *Linnaea borealis*, *Arnica cordifolia*, *Cornus canadensis* and feathermoss distinguish a number of cluster divisions. Stands which were quite dissimilar to adjacent clusters containing several highly abundant species are often placed between them (e.g. stands 4 & 14) and thus the sequence on Figure 8 does not follow a strictly ecological gradient. The over-riding influence of one or two highly abundant species in delimiting clusters was not considered a desirable attribute of the cluster analysis. The ordination technique appears to give a better indication of stand relationships since no rigid boundaries are employed. However, many of the same groups were delimited by both methods (Figs. 8 & 9). Both techniques, along with tree seedling and transgressive class data (Appendix 2) were used in establishing the components of the series and h.t.s.

The ordination methods follow the modified techniques outlined by Beals (1960) and Maycock and Curtis (1960). The technique is somewhat handicapped, however, when the community *(beta)* diversity (range of communities in the sample) is high since distortion from linear relationships is encountered (Gauch & Whittaker 1972). Also, high *beta* diversity

Figure 9. Ordination of the 35 stands with 5 and 34 selected as the ends of the x-axis. Stand 5 had the highest total similarity coefficient with the rest of the stands and stand 34 had the lowest value to stand 5. The cluster groupings from Figure 8 are indicated where possible. The mixed character of a number of montane stands are indicated by the lack of correlation between cluster and ordination groups.


SUBALPINE
MONTANE
II
X
V
IX
VI
VII
VII
Y
X

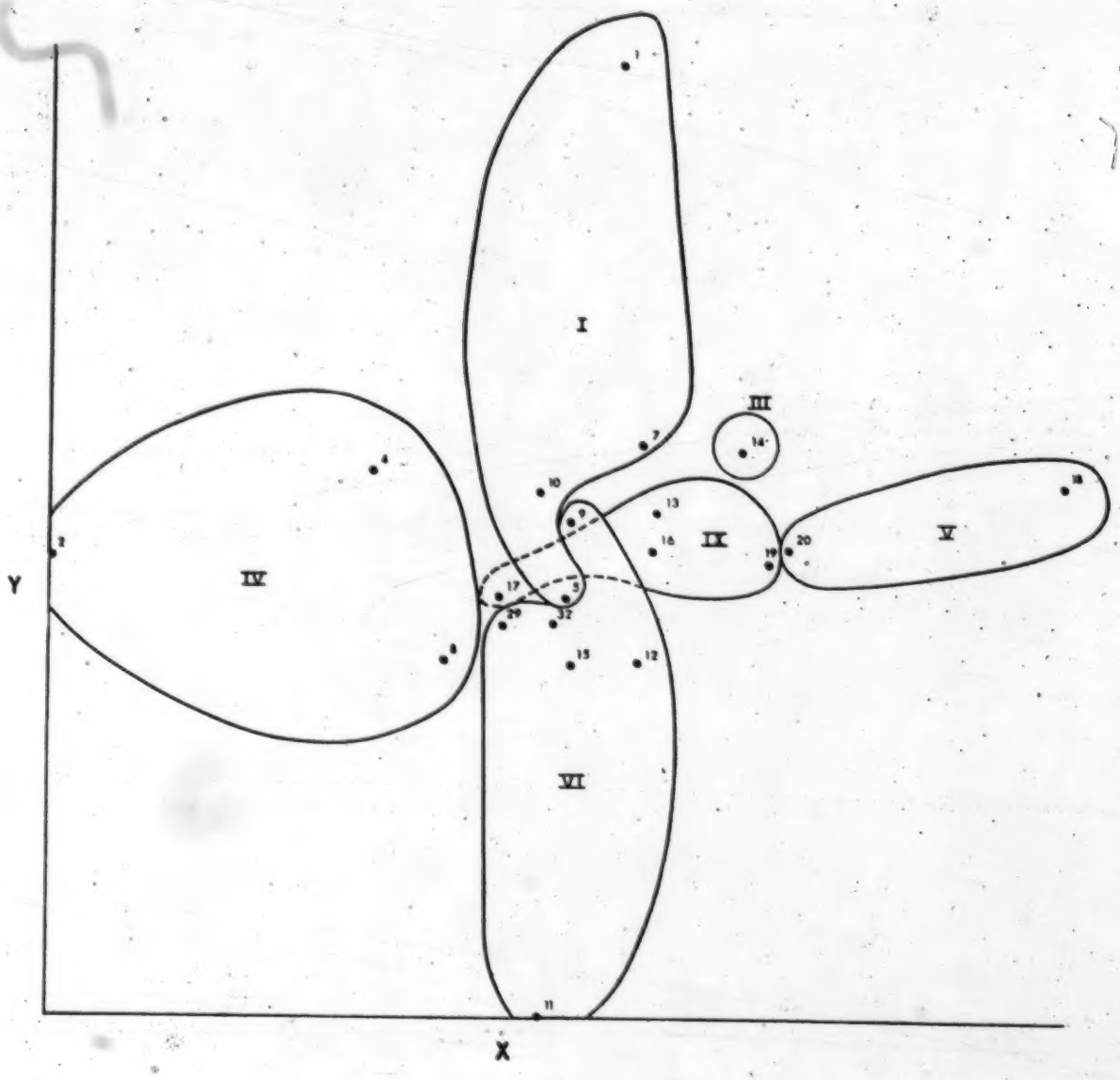
causes the ordination to be less interpretive since many of the more similar stands will be tightly clustered. This problem was noted by Stringer (1973), and end stands were chosen using a "similarity principle" instead of the usual most dissimilar stands for plotting the structure of the x-axis. Thus, according to Stringer, "the more species the end stand has in common with the other stands, the more accurately they could be placed on the axis". Better separation of the 35 stands was obtained using this method, but the montane stands were still centrally located (Fig. 9). An additional ordination of only this central cluster with no end stand designation delimited groups which conformed for the most part into the proposed montane Series and h.t.s (Fig. 10). Both ordinations had significant correlations between stand similarity coefficients and distance on the field ($r = -0.60$, all stands; $r = -0.86$ central cluster; $p < 0.05$).

6.3 The Habitat Types (h.t.) of Vine Creek Basin

6.3.1 Montane Scrubland

Scrub communities composed primarily of shrub and graminoid species occupy warm and relatively xeric portions of the basin, occurring on the steep (15 - 20°) S-facing slopes of glaciofluvial terraces (Table 11). Elevations of the sampled sites ranged from 1070 to about 1200 m, and thus the communities occurred as small units within the larger montane forest. Smaller fragments of the vegetation occurred above this on S -facing slopes but usually other more mesophytic species were also evident. The vegetation was represented by one association.

Figure 10. Ordination of selected stands comprising the *Picea* and *Pseudotsuga* Series, or most of the central cluster in Figure 9. The cluster groupings from Figure 8 are indicated, but some stands of the clusters were not included on the ordination.


I
II
III
IV
V
VI
VII
VIII
IX
Y
X

6.3.1.1 *Arctostaphylos uva-ursi - Calamagrostis purpurascens* h.t.

The h.t. was represented by Cluster VII (stands 3 & 6) in Figure 8 and was distinctly separated from the rest of the stands on the ordination (stands 3 & 6, Fig. 9). *Pseudotsuga menziesii* was usually associated with the h.t., but was scattered and mainly confined to ravines which dissect the slopes. *Populus tremuloides* and *Picea glauca* also occurred in these ravines, but were less common (see Fig. 1, p. 21, for stand locations).

The shrub stratum was quite open, having a mean cover of 10%, most of which was from *Juniperus communis* and *Rosa acicularis* (Table 11). Herb and low shrub species were more abundant having a mean cover of 54%. *Arctostaphylos uva-ursi* was the dominant having a mean cover of 34% and occurred as a prominent and diagnostic feature of the h.t. (Plate 2). Other prominent species included *Calamagrostis purpurascens, Galium boreale, Artemisia frigida* and *Solidago decumbens*. *G. boreale* had a higher mean cover than *Calamagrostis purpurascens* and was probably one of the diagnostic species in defining the cluster, but was not used in the association nomenclature since it was visually less dominant. *Stipa comata, Agropyron latiglume* and *Koeleria cristata* exhibited low cover (1%), but together produced a grassland physiognomy where *A. uva-ursi* was less dominant (Plate 2).

The bryoid layer was sparse with only *Tortella tortuosa, Thuidium abietinum* and *Polytrichum juniperinum* having mean cover near 1%. *Cladonia phyllophora* and *Eurhynchium pulchellum* were also present (Table 11).

Table 11. Physical characteristics and ground cover values of major species basin. Species listed are mainly those having presence values > 6% except contained important but restricted species.

	MONTANE SCRUBLAND		PSEUDOTSUGA SERIES								PICEA SERIE						
	Au-u-Cp		Pm/Jc/Cp			Pm/Ei					Pg/Cv-Lb	Pg/Lb/Hs			Pg/Ei/Cc		
STAND	3	6	2	8	4	17	9	11	12	15	1	5	7	10	14	13	18
SLOPE ANGLE - DEGREES	15	20	3	4	2	20	10	29	12	19	-	3	6	29	9	15	7
SLOPE ASPECT	S	S	NE	SW	WSW	SW	SE	ESE	WSW	WSW	-	SE	WSW	E	E	ESE	S
ELEVATION (m ASL)	1070	1140	1050	1195	1075	1470	1200	1300	1320	1400	1000	1130	1150	1280	1360	1330	1495
SPECIES																	
TREE STRATUM																	
PICEA GLAUCA	-	-	8	-	9	3	6	5	1	2	60	2	19	20	5	1	-
PSEUDOTSUGA MENZIESII	-	1	5	6	27	8	20	5	22	10	-	8	29	29	1	2	-
PINUS CONTORTA	-	-	13	13	11	32	46	48	43	36	-	50	2	9	57	37	32
POPULUS TREMULOIDES	-	-	-	1	-	-	1	-	1	8	-	-	-	-	-	-	-
PICEA MARIANA	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	1
PICEA GLAUCA X ENGELMANNII	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
ABIES LASIOCARPA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PICEA ENGELMANNII	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PINUS ALBICAULIS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SHRUB STRATUM																	
PICEA GLAUCA	-	-	1	2	1	1	1	-	-	-	1	1	11	2	1	5	2
PSEUDOTSUGA MENZIESII	-	-	1	5	5	4	t	t	t	1	-	1	1	t	t	1	-
PINUS CONTORTA	-	-	-	2	-	1	t	-	-	t	-	-	-	-	1	1	-
PICEA GLAUCA X ENGELMANNII	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ABIES LASIOCARPA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PICEA ENGELMANNII	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
JUNIPERUS COMMUNIS	2	8	12	12	12	3	2	4	2	t	-	8	t	2	1	-	-
ROSA ACICULARIS	8	1	1	1	1	5	1	2	1	5	1	3	3	2	1	3	-
SHEPHERDIA CANADENSIS	-	-	5	4	1	7	3	2	1	4	-	2	2	-	10	11	1
ALNUS CRISPA	-	-	-	-	-	4	-	-	-	-	-	4	t	-	t	8	1
A. TENUIFOLIA	-	-	-	-	-	t	-	-	-	-	-	-	-	-	3	-	-
AMELANCHIER ALNIFOLIA	-	-	-	-	-	8	-	-	-	-	3	-	-	-	t	5	-
SPIRAEA LUCIDA	-	-	-	-	-	-	1	1	2	1	-	2	-	7	-	-	-
VIBURNUM EDULE	-	-	-	-	-	-	t	-	-	-	1	-	1	t	-	2	-
SYMPHORICARPOS ALBUS	-	-	-	-	-	-	-	t	-	-	-	3	t	t	-	-	-
SALIX BEBBIANA	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	t	t
VACCINIUM MEMBRANACEUM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	t
S. GLAUCA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	t
LEDUM GROENLANDICUM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	t	6
MENZIESIA GLABELLA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
RHODODENDRON ALBIFLORUM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HERB AND LOW SHRUB STRATUM																	
CAREX VAGINATA											8						
APOCYNUM ANDROSAEMIFOLIUM	1	1	5	7	6	-	-	-	-	-	-	-	t	-	-	t	-
GALIUM BOREALE	5	2	t	1	t	2	1	1	t	t	1	1	1	-	t	-	-
ARCTOSTAPHYLOS UVA-URSI	38	30	7	3	3	4	t	-	-	-	-	-	-	t	-	1	-
ARTEMISIA FRIGIDA	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ERIGERON COMPOSITUS	1	2	1	t	-	-	-	t	-	-	-	-	-	-	-	-	-
CALAMAGROSTIS PURPURASCENS	3	5	20	25	18	-	-	-	-	-	-	-	8	-	-	-	-
ASTER CILIOLATUS	1	1	-	-	-	1	-	-	-	-	-	-	4	-	-	-	-
LATHYRUS OCHROLEUCUS	t	t	3	10	t	2	1	-	t	t	-	1	2	-	10	-	-
ELYMUS INNOVATUS	t	1	-	7	2	29	11	8	4	10	-	8	7	4	7	18	15
HEDYSARUM MACKENZII	t	1	-	1	-	-	-	t	-	t	-	-	-	-	-	-	-

Physical characteristics and ground cover values of major species comprising the h t s in the Vine Creek
Species listed are mainly those having presence values > 85 except in the subalpine shrub meadows which
d important but restricted species

SERIES				PICEA - SERIES												PICEA ENGELMANNII - ABIES LASIOCARPA SERIES										SUBALPINE SHRUB MEADOW			
Pm/Ei				Pg/Cw-Lb		Pg/Lb/Hs			Pg / Ei / Cc			P/Ak/Ei			▫ P-Pa/Ac/Ei		Pe-Al/Mg-Vm						Pe-Al/Ac		Pe-Al/Ad/Hs		Sg/Ei		Sv/Pa	
9	11	12	15	1		5	7	10	14	13	18	20	19	16	29	32	21	22	23	24	25	27	28	30	31	33	26	34	35
10	29	12	19	-		3	6	29	9	15	7	27	23	23	30	33	18	19	19	10	9	11	6	15	28	33	3	6	3
SE	ESE	WSW	WSW	-		SE	WSW	E	E	ESE	S	E	SW	NE	SW	SW	NE	NE	WSW	SW	W	SSW	SSW	NE	SW	NE	SE	NE	NE
1260	1300	1320	1400	1000		1130	1150	1280	1360	1330	1495	1570	1530	1430	1740	1900	1600	1610	1615	1615	1635	1680	1720	1770	1840	2040	1670	2075	2060
6	5	1	2	60		2	19	20	5	4	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20	5	22	10	-		8	28	29	1	2	-	1	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
48	48	43	36	-		50	2	9	57	37	32	28	55	50	20	7	15	20	-	-	-	1	-	-	-	-	-	-	-
1	-	1	8	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-		-	-	-	-	-	1	-	1	1	t	-	1	2	t	2	2	-	1	1	-	-	-	-	-
-	-	-	-	-		-	-	-	-	-	8	13	1	-	29	-	9	18	31	-	-	-	-	-	25	-	-	-	-
-	-	-	-	-		-	-	-	-	-	-	-	1	-	2	6	1	2	21	8	24	21	18	28	5	47	-	-	-
-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	25	-	-	-	35	30	27	35	27	-	13	-	-	-
-	-	-	-	-		-	-	-	-	-	-	-	-	-	2	11	-	-	-	-	-	-	-	-	21	-	-	-	-
1	-	-	-	1		1	11	2	1	5	2	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1	t	t	1	-		1	1	t	t	1	-	-	-	-	8	2	t	-	-	-	-	-	-	-	-	-	-	-	-
t	-	-	1	-		-	-	-	1	1	-	t	-	26	1	1	4	2	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-		-	-	-	-	-	-	1	-	-	1	1	t	1	1	t	3	-	14	26	t	3	-	t	-
-	-	-	-	-		-	-	-	-	-	-	-	-	-	t	t	-	t	-	12	1	1	2	2	-	-	1	-	-
2	4	2	t	-		6	t	2	1	-	-	8	-	-	11	11	1	-	t	2	-	-	-	-	-	-	-	-	-
1	2	1	5	1		3	3	2	1	3	-	1	38	5	1	1	-	-	-	-	-	-	-	-	1	-	-	-	-
3	2	1	4	-		2	2	-	10	11	t	-	3	9	3	t	3	2	2	1	-	-	-	-	-	-	-	-	-
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	MONTANE SCRUBLAND		PSEUDOTSUGA SERIES								PICEA S						
	Au-u-Cp		Pm/Jc/Cp			Pm/Ei					Pg/Cw-Lb	Pg/Lb/Hs			Pg/Ei/Cc		
STAND	3	6	2	8	4	17	9	11	12	15	1	5	7	10	14	13	18
SLOPE ANGLE - DEGREES	15	20	3	4	2	20	10	29	12	19	-	3	6	29	9	15	7
SLOPE ASPECT	S	S	NE	SW	WSW	SW	SE	ESE	WSW	WSW	-	SE	WSW	E	E	ESE	S
ELEVATION (m ASL)	1070	1140	1050	1195	1075	1470	1200	1300	1320	1400	1000	1130	1150	1280	1360	1330	1490
SPECIES																	
HERB AND LOW SHRUB STRATUM (cont'd)																	
ACHILLEA MILLEFOLIUM	t	t	t	-	-	-	-	-	-	-	-	-	-	-	-	12	
CASTILLEJA MINIATA	t	-	-	t	-	3	-	t	-	t	-	t	-	t	t	t	
ANEMONE MULTIFIDA	t	-	t	t	t	t	-	-	-	t	-	-	-	-	-	-	
CAMPANULA ROTUNDIFOLIA	t	t	t	-	-	-	-	-	-	-	-	-	-	-	-	-	
ERIGERON CAESPITOSUS	t	-	t	t	-	2	-	-	-	-	-	-	-	-	t	-	
LINNAEA BOREALIS	t	-	-	8	13	13	13	6	8	5	14	14	11	7	3	17	5
SOLIDAGO DECUMBENS	-	4	-	-	-	-	-	2	t	t	-	t	-	-	-	-	
EPILOBIUM ANGUSTIFOLIUM	-	-	t	-	-	-	-	-	-	t	-	-	-	-	1	1	
DISPORUM TRACHYCARPUM	-	-	-	t	t	-	1	-	-	t	-	t	3	t	-	-	
PYROLA SECUNDA	-	-	-	t	t	-	t	-	t	-	-	t	-	-	t	4	
CAREX RETRORSA	-	-	-	3	-	-	-	1	t	2	-	-	-	-	-	-	
ERIGERON PEREGRINUS	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	
HABENARIA HYPERBOREA	-	-	-	-	t	-	1	-	t	-	t	-	t	-	-	1	
ASTER CONSPICUUS	-	-	-	-	2	5	3	t	1	2	t	1	7	2	t	10	3
ARNICA CORDIFOLIA	-	-	-	-	-	t	-	-	t	t	-	t	3	-	8	4	
CAREX CONCINNA	-	-	-	-	-	2	-	-	-	-	-	-	1	-	-	-	
LYCOPODIUM ANNOTINUM	-	-	-	-	-	-	t	-	-	-	-	-	-	-	t	-	
CLEMATIS VERTICELLARIS	-	-	-	-	-	-	1	-	t	1	-	-	-	-	2	2	
PYROLA VIRENS	-	-	-	-	-	-	-	t	-	-	-	t	-	t	t	-	
CORNUS CANADENSIS	-	-	-	-	-	-	2	-	-	-	-	t	8	t	7	7	9
GEOCAULON LIVIDUM	-	-	-	-	-	-	t	-	-	-	t	-	2	-	-	-	
MITELLA NUDA	-	-	-	-	-	-	t	-	-	-	t	t	2	-	t	-	
PYROLA ASARIFOLIA	-	-	-	-	-	-	-	-	-	t	t	-	-	-	t	-	t
VACCINIUM CAESPITOSUM	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	7
SOLIDAGO MULTIRADIATA	-	-	-	-	-	-	-	-	-	-	-	-	-	t	t	-	
EQUISETUM SCIRPOIDES	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	
PEDICULARIS BRACTEOSA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	t	
AQUILEGIA FLAVESCENS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	
EQUISETUM ARVENSE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
VACCINIUM SCOPARIUM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
ARCTOSTAPHYLOS RUBRA	-	-	-	-	-	-	-	-	1	8	-	t	-	-	-	-	
TRISETUM SPICATUM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
ARNICA DIVERSIFOLIA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
PHLEUM ALPINUM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
ARTEMISIA NORVEGICA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
POLYGONUM VIVIPARUM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
POA ALPINA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
SALIX BARRATTIANA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
CAREX PHAEOCEPHALA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
LUZULA SPICATA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
CAREX NIGRICANS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
PARNASSIA FIMBRIATA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
CAREX ATROSQUAMA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
CAREX NARDINA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
CASSIOPE MERTENSIANA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
POA PRATENSIS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
JUNCUS DRUMMONDII	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
ARNICA MOLLIS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	

Table 11 (Continued)

UGA SERIES					PICEA SERIES												PICEA ENGELMANNII - ABIES LASIOCARPA SERIES										SUBALPINE SHRUB MEADOW		
Pm/Ei					Pg/Cw-Lb	Pg/Lb/Hs			Pg / Ei / Cc			P/Alc/Ei			P-Pa/Jc/Ei		Pe-Al/Mg-Vm						Pe-Al/Ac		Pe-Al/Ad/Hs		Sg/Ei	Sv/Po	
7	9	11	12	15	1	5	7	10	14	13	18	20	19	16	29	32	21	22	23	24	25	27	28	30	31	33	26	34	35
0	10	29	12	19	-	3	6	29	9	15	7	27	23	23	30	33	18	19	19	10	9	11	6	15	28	33	3	6	3
W	SE	ESE	WSW	WSW	-	SE	WSW	E	E	ESE	S	E	SW	NE	SW	SW	NE	NE	WSW	SW	W	SSW	SSW	NE	SW	NE	SE	NE	NE
70	1200	1300	1320	1400	1000	1130	1150	1280	1360	1330	1495	1570	1530	1430	1740	1900	1600	1610	1615	1613	1633	1680	1720	1770	1840	2040	1670	2075	2060
										12					t	t	-	t	-	-	-	-	-	-	-	-	1	t	3
3	-	t	-	t	-	t	-	t	t	t	-	t	t	-	t	t	-	-	-	-	-	-	-	-	-	-	-	-	-
t	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	t	-	-	t	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	-	t	-	-	-	-	3	t	t	-	-	-	-	-	-	-	-	-	-	-	-	-
13	13	8	8	5	14	14	11	7	3	17	5	3	5	17	4	4	3	t	t	2	2	2	t	-	-	t	-	-	-
-	-	2	t	t	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	t	-	-	-	-	t	t	t	t	t	t	t	t	3	t	-	t	t	t	-	-	-	t	-	-	-
-	t	-	-	-	-	t	3	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	t	-	-	-	-	t	-	-	t	4	-	t	-	-	t	t	-	-	t	5	t	t	8	3	t	t	-	-	-
-	-	t	t	2	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	2	-	2
-	t	-	t	-	-	t	-	t	-	t	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	3	t	t	2	-	t	7	2	t	10	3	t	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
t	-	-	t	t	-	t	3	-	8	4	3	4	10	2	4	2	2	t	3	t	t	2	8	9	-	-	-	-	-
2	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-
-	t	-	-	-	-	-	-	-	t	-	t	-	-	-	-	-	t	-	-	-	t	2	2	8	-	3	-	-	-
-	t	-	t	t	-	-	-	-	2	2	-	t	t	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	t	-	-	-	t	-	t	t	-	-	-	t	3	t	t	-	-	t	-	-	t	-	-	-	-	-	-	-
-	2	-	-	t	-	t	8	t	7	7	8	3	2	8	-	-	15	3	t	3	3	3	10	2	2	-	-	-	-
-	t	-	-	-	t	-	2	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	t	-	-	-	t	t	2	-	t	-	-	-	-	t	-	-	-	-	-	t	t	-	-	-	-	-	-	-	-
-	-	-	-	t	t	-	-	-	t	-	t	-	-	-	-	-	t	-	-	-	t	-	t	-	t	-	-	-	-
-	-	-	-	-	-	-	t	-	-	-	7	-	t	-	-	-	-	3	t	-	3	t	-	-	-	t	t	-	-
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-	-	-	-	-	-	-	-	-	-	t	-	t	t	-	-	t	t	-	-	-	-	-	-	-	-	-	-	-	-
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2 of 2

	MONTANE SCRUBLAND Au-u-Cp		PSEUDOTSUGA SERIES Pm/Jc/Cp			Pm/Ei					PICEA SER Pg/Cw-Lb	Pg/Lb/Hs			Pg/Ei/Cc		
STAND	3	6	2	8	4	17	9	11	12	15	1	5	7	10	14	13	18
SLOPE ANGLE - DEGREES	15	20	3	4	2	20	10	29	12	19	-	3	6	29	9	15	7
SLOPE ASPECT	S	S	NE	SW	WSW	SW	SE	ESE	WSW	WSW	-	SE	WSW	E	E	ESE	S
ELEVATION (m ASL)	1070	1140	1050	1195	1075	1470	1200	1300	1320	1400	1000	1130	1150	1280	1360	1330	1495
SPECIES																	
PLANTAGO MAJOR																	
BRYOPHYTE STRATUM																	
THUIDIUM ABIETINUM	2	1	2		6						10		1				
CLADONIA PHYLLOPHORA	2						1		1	1	1						
HYLOCOMIUM SPLENDENS			1	10	16	20		2	2	2	50	30	57	54	47	23	18
PELTIGERA CANINA			1	5	3	5	5		1		1	1	2	25			1
DISTICHIUM CAPILLACEUM			1								1	1					
CLADONIA CORNUTA				1	1				1				1				1
PLEUROZIUM SCHREBERI					11	1	1		1	1		13	38	22	6	3	6
DREPANOCLADUS REVOLVENS					1						1		1				
CLADONIA CHLOROPHAEA					1	1	1	1		1		1	1	1			
CETRARIA NIVALIS					1				1								
PELTIGERA APHTHOSA								1					3				
CLADONIA GRACILIS								1			1						2
C ECMOCYNA													1				
PTILIUM CRISTA CASTRENSIS															50	5	
ALECTORIA GLABRA																	1
POHLIA NUTANS																	1
DICRANUM POLYSETUM														1		1	1
DREPANOCLADUS UNCINATUS															1		1
ICMADOPHILA ERICETORUM																	
SPHAGNUM WARNSTORFII																	
CLADONIA GONECHA																	
AULACOMNIUM PALUSTRE																	
CLADONIA FIMBRIATA																	
BARBILOPHOZIA SP																	

UGA SERIES					PICEA SERIES												PICEA ENGELMANNII - ABIES LASIOCARPA SERIES										SUBALPINE SHRUB MEADOW		
Pm/Ei					Pg/Cw-Lb		Pg/Lb/Hs			Pg/Ei/Cc			P/Al/Ei			P-Po/Jc/Ei		Pe-Al/Mg-Vm						Pe-Al/Ac		Pe-Al/Ad/Hs		Sg/Ei	Sv/Fd	
17	9	11	12	15	1		5	7	10	14	13	18	20	19	16	29	32	21	22	23	24	25	27	28	30	31	33	26	34	35
20	10	29	12	19	-		3	6	29	9	15	7	27	23	23	30	33	18	19	19	10	9	11	6	15	28	33	3	6	3
W	SE	ESE	WSW	WSW	-		SE	WSW	E	E	ESE	S	E	SW	NE	SW	SW	NE	NE	WSW	SW	W	SSW	SSW	NE	SW	NE	SE	NE	NE
670	1200	1300	1320	1400	1000		1130	1150	1280	1360	1330	1495	1570	1530	1630	1780	1900	1600	1610	1615	1613	1633	1680	1720	1770	1840	2040	1670	2075	2060
					10			1									1								1					
	1		1	1	1									1				8	5	1			1							
20		2	2	2	50		38	57	54	47	23	18	17	2	11	2	2	13	11	80	65	71	71	54	50	11	13			
5	5		1		1		1	2	25			1			1						6									1
					1		1							1		1	1			4		4			1	1			1	2
			1					1				1			1				1						1					
1	1		1	1			13	38	22	8	1	6		3	2				1	8	8	13	18	21	18	3	2			
					1			1										2								2			
1	1	1		1			1	1	1							1					1		1			1	2			
			1											1																
		1						3							1		1	4	1	3			1	10	8	1	2		2	1
		1			1							2	1					2	1						1					
								1							3	1		1	1	1	1	1		4	2	1	1		2		
										50	1					1	1			1		2	4	9	8					
												1		1		1	1		1	1						1				
												1							2						1					2
									1		1	1	1																	
										1		1	1	1	1	1					1		1		1					
																2														
																					1		1		1					
																					5			4		2		12	8	8
																						2		5			1			
																							12							
																							17							
																								2	8					

Plate 2. Montane scrubland of the steep S exposed slopes containing the *Arctostaphylos uva-ursi - Calamagrostis purpurascens* h.t. (stand 6).

The h.t. is postulated as having a topographic climax and is confined to steep S-facing slopes. Modification by bighorn sheep grazing, especially in winter, is apparently significant with numerous trails contouring the area, and this may reduce the grass cover in favor of the low shrubs (Plate 2). Fire evidence occurred only as charcoal on older *Pseudotsuga menziesii*, but is probably not a major inhibiting factor in tree regeneration since very few seedlings were present.

6.3.2 *Pseudotsuga menziesii* Series

The h.t.s of this Series were mostly occupied by subclimax forests dominated by *Pinus contorta*. Using the effective stand age (ESA) and mean ages of *P. contorta*, stand development appeared to follow 1895 and 1910 fires, though trees from stand 11 appeared to date from about 1870 (Table 12). Pre-fire relicts were present in most of the stands, and thus exact dates of stand origin were difficult to determine.

Picea glauca occurred in all but one of the eight stands, and in stands 2 and 9 had greater seedling and transgressive density than *Pseudotsuga menziesii* (see Fig. 1, p. 21, for stand location). The latter species, however, was usually more consistently represented throughout the size class range (Appendix 2). Separation of the stands from the *Picea* Series was aided by the cluster analysis and ordination positioning, and an affinity of the understory composition toward the more definite *Pseudotsuga* group (Figs. 8, p. 96 & 9, p. 99). A second ordination of the central group on Figure 10 was especially helpful in making final delimitations. *Populus tremuloides* occurred in some of the

Table 12. Age characteristics of the Vine Creek habitat types based on effective stand age (ESA, see Methods, p. 37), mean age and maximum ages of the component species. More mature vegetation is usually indicated by a greater disparity between $\bar{X}$ and maximum ages, but a wide range also occurs in stands containing pre-fire relicts.

HABITAT TYPE	STAND NO.	ESA	Pg		Pm		Pc		Pgxe		Al		Pe		Pa	
			$\bar{X}$	MAX	$\bar{X}$	MAX	$\bar{X}$	MAX	$\bar{X}$	MAX	$\bar{X}$	MAX	$\bar{X}$	MAX	$\bar{X}$	MAX
Pseudotsuga menziesii / Juniperus communis / Calamagrostis purpurascens	2	56	-	-	40	125	68	73	-	-	-	-	-	-	-	-
	8	77	-	-	69	76	69	88	-	-	-	-	-	-	-	-
	4	72	62	74	128	191	67	82	-	-	-	-	-	-	-	-
P. menziesii / Elymus innovatus	17	56	-	50	68	74	52	62	-	-	-	-	-	-	-	-
	9	67	-	67	-	62	75	80	-	-	-	-	-	-	-	-
	11	91	-	-	75	80	83	103	-	-	-	-	-	-	-	-
	12	72	-	-	79	120	66	77	-	-	-	-	-	-	-	-
	15	72	-	-	63	71	54	80	-	-	-	-	-	-	-	-
Picea glauca / Carex vaginata - Linnaea borealis	1	203	164	288	-	-	-	-	-	-	-	-	-	-	-	-
P. glauca / Linnaea borealis / Hylocomium splendens	5	79	-	-	55	59	64	90	-	-	-	-	-	-	-	-
	7	233	199	281	204	232	140	173	-	-	-	-	-	-	-	-
	10	122	66	68	136	286	110	192	-	-	-	-	-	-	-	-
Picea / Elymus innovatus / Cornus canadensis	14	52	40	50	-	-	48	60	-	-	-	-	-	-	-	-
	13	49	48	50	-	45	49	55	-	-	-	-	-	-	-	-
	18	54	-	-	-	-	46	50	90	134	-	-	-	-	-	-
Picea / Alnus crispa / Elymus innovatus	20	46	-	-	-	-	46	50	90	134	-	-	-	-	-	-
	19	48	-	-	-	-	43	53	-	-	-	-	-	-	-	-
	16	53	-	-	-	-	52	60	-	-	-	-	-	-	-	-
Picea - Pinus albicaulis / Juniperus communis / Elymus innovatus	29	196	-	-	-	-	55	72	99	101	-	-	-	-	-	210
	32	131	-	-	-	-	86	119	-	-	-	-	99	133	162	220
Picea engelmannii - Abies lasiocarpa / Menziesia glabella / Vaccinium membranaceum	21	51	-	-	-	-	51	55	37	39	-	-	-	-	-	-
	22	49	-	-	-	-	53	103	38	47	-	-	-	-	-	-
	23	236	-	-	-	-	-	267	203	265	216	223	-	-	-	-
	24	198	-	-	-	-	-	-	-	-	104	150	144	245	-	-
	25	199	-	-	-	-	-	-	-	-	147	177	207	238	-	-
	27	175	-	-	-	-	-	-	-	-	136	168	200	245	-	-
P. engelmannii - A. lasiocarpa / Arnica cordifolia	28	207	-	-	-	-	-	-	-	-	122	168	215	245	-	-
	30	196	-	-	-	-	-	-	-	-	175	200	208	220	-	-
P. engelmannii - A. lasiocarpa / Arnica diversifolia / Hylocomium splendens	31	192	-	-	-	-	-	-	-	-	-	121	-	217	164	191
	33	111	-	-	-	-	-	-	-	-	97	132	173	184	-	-

stands, but was usually associated with alluvium deposition at the base of the constant slope.

6.3.2.1 *Pseudotsuga menziesii/Juniperus communis/Calamagrostis purpurascens* h.t.

This h.t. type, represented by stands 2, 4 and 8, occurred on alluvial terraces and SW-facing benches between about 1000 and 1200 m elevation. The stands were distinct from the others on the cluster analysis and ordination (Figs. 8 & 9). The h.t. appeared to be xeric, having coarse, rapidly drained soils and the lower stand was on a boulder substrate and is illustrated in Plate 3. Ground water may reduce the aridity of the sites on the alluvial terraces at least for deep-rooted species.

The tree stratum was fairly open, with a mean cover of 31%, for the h.t. and this composed of nearly equal quantities of *Pseudotsuga menziesii* and *Pinus contorta*. Tree (> 4 cm dbh) density had a mean for the h.t. of 3315 stems ha^{-1} with most of these between 8 and 23 cm dbh, but some *P. menziesii* extend to 53 cm dbh (tree statistics for all h.t.s are listed in Appendix 2). Mean basal area for the h.t. was 26 m^2 ha^{-1} with *P. menziesii* and *P. contorta* comprising 38 and 46% of the total respectively.

The shrub stratum was visually quite prominent with a cover of 22%, most of which was from two species - *Juniperus communis* and *Shepherdia canadensis* (Table 11). Minor species of the stratum included *Picea glauca*, *Pseudotsuga menziesii*, *Pinus contorta* and *Rosa acicularis*.

Plate 3. The *Pseudotsuga menziesii* series with *P. menziesii/Juniperus communis/Calamagrostis purpurascens* h.t. (stand 2; A) and the *P. menziesii/Elymus innovatus* h.t. (stand 12; B).

A

B

The herb and low shrub stratum was uniformly dominated by *Calamagrostis purpurascens* (cover of 21%), with a number of other species including *Arctostaphylos uva-ursi, Apocynum androsaemifolium,* and *Lathyrus ochroleucus* also characterizing the h.t. (Table 11, p. 105). Other less abundant but constant species included *Anemone multifida, Galium boreale, Elymus innovatus, Linnaea borealis, Erigeron compositus* and *Antennaria nitida,* the last two indicating disturbance.

Dominants of the bryoid layer included *Hylocomium splendens, Peltigera canina* and *Thuidium abietinum;* these constituted most of the 20% cover. Minor species included *Pleurozium schreberi* and *Cladonia cornuta* (Table 11).

The sampled stands represent a relatively immature community with ages of the trees confined to a narrow range (Table 12). Stands (4, 8) probably originated from fires which occurred between 1890 and 1895. Compared with older stands on other h.t.'s of the Series, a decrease in shrub cover is postulated with more development toward the association. The rocky substrate may retard vegetative ground cover development, however, and the h.t. is clearly represented by an edaphic climax.

6.3.2.2 *Pseudotsuga menziesii/Elymus innovatus* h.t.

Five stands (17, 9, 11, 12, 15) were delimited from the rest of the *Pseudotsuga* Series on the ordination and represent the h.t. (see Fig. 9, p. 100. The stands were subclimax with *Pinus contorta* the dominant tree. The h.t. included moderate to steep portions of the constant

colluvial slope between 1200 and 1500 m elevation (Table 11, p. 105). Surface run-off from adjacent ridges has caused some ravine formation especially in the higher stands, and colluvial-alluvial deposition occurred below this near the base of the valley slope. The h.t. is illustrated in Plate 3 (stand 12).

The tree stratum was relatively dense with a h.t. mean cover of 65%, and thus was more comparable to forests in the *Picea* Series. *Pseudotsuga menziesii* accounted for only 16% of this total. Tree density was 3216 stems ha^{-1} with the majority in the sapling (4 - 8 cm dbh) size class. The largest trees were *P. menziesii* which ranged up to 46 cm dbh and 22 m high. Mean basal area was 35 m^2 ha^{-1} with *P. menziesii* and *Pinus contorta* comprising 25 and 68% of the total respectively.

Stands varied in age from 56 to 91 years for the h.t., and judging from the maximum age of *P. contorta*, probably originated after an 1895 fire (Table 12). Stand 11 was the exception and probably dates from an earlier fire (ca 1870). The wide range between maximum and mean effective stand ages reflected older pre-fire relicts of both *P. menziesii* and *P. contorta* (Table 12).

The shrub stratum was relatively depauperate having a cover of 16%. *Juniperus communis*, *Shepherdia canadensis*, *Rosa acicularis* and *Spiraea lucida* were the more prominent species (Table 11). The herb and low shrub stratum had a higher cover (37%), but was more open than the understory of the *Pm/Jc/Cp* h.t. *Elymus innovatus*, along with *Linnaea*

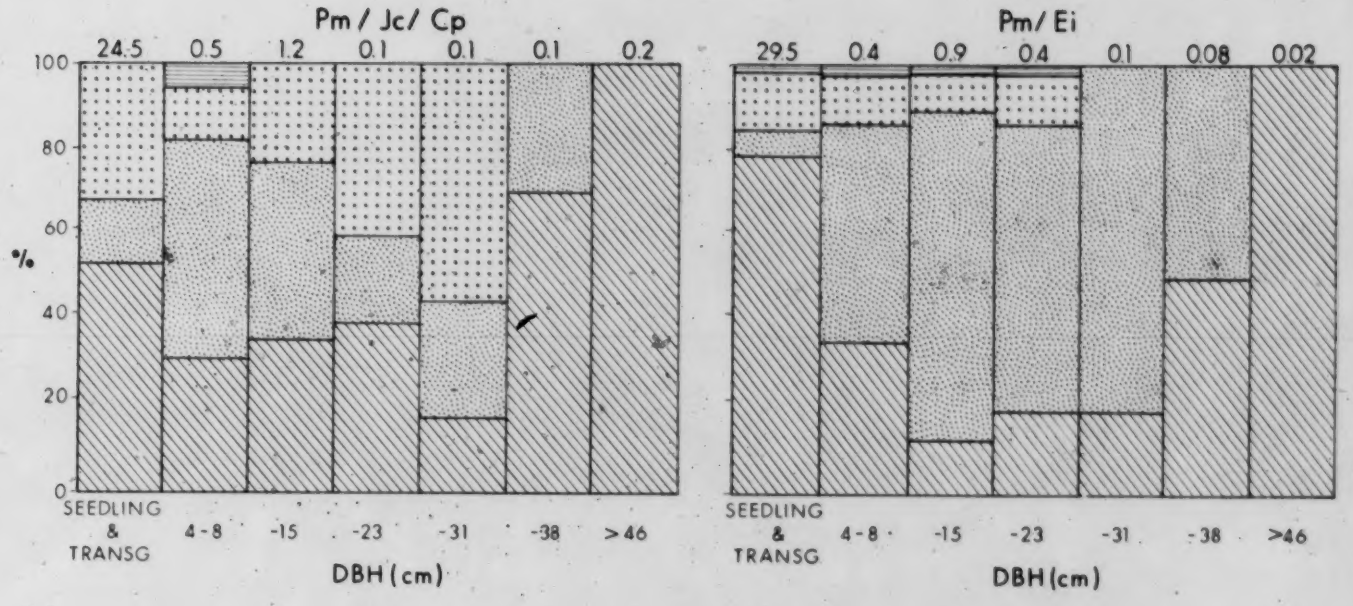
borealis, however, formed a luxuriant ground cover (Plate 3). Other characteristic but minor species included *Aster conspicuus*, *Galium boreale*, *Solidago decumbens* and *Clematis verticellaris* (Table 11, p. 105).

The open nature of the understory was reflected by the low bryophyte cover (9%). *Hylocomium splendens*, *Pleurozium schreberi*, *Peltigera canina*, *Cladonia phyllophora* and *C. chlorophaea* were the most abundant species of the stratum (Table 11, p. 105). The low moss and lichen cover may be a function of a thick *P. contorta* needle layer and warm, xeric nature of the h.t.

6.3.2.3 Size distribution of trees in the *Pseudotsuga* series

Pseudotsuga menziesii was dominant in the smaller size classes, indicating a successional trend toward the association (Fig. 11). Although *Pinus contorta* also occurred in the seedling and transgressive categories, it was more common as a sapling, extending into the large diameter classes in the *Pseudotsuga/Elymus* h.t. *Picea glauca* was relatively more common in the *Pseudotsuga/Juniperus/Calamagrostis* h.t., which occurred closer to the valley floor on alluvium. In both h.t.s, *P. menziesii* exhibited a bimodal size distribution, occurring predominantly as seedlings and as large pre-fire relicts. Between these extremes was a more normally distributed *P. contorta* population (Fig. 11). The *Pseudotsuga/Elymus* community was the older of the two, but age data were similar enough (Table 12, p. 111) so that a less xeric site condition, may be more important than fire history, in accounting for the larger *P. contorta* population in this h.t.

Figure 11. Histograms showing the size class distribution of the major tree species within the *Pseudotsuga menziesii* Series. Tree density (stems ha^{-1} X 100) is given above each category.



TREE SPECIES LEGEND

- *Pseudotsuga menziesii*
- *Pinus contorta*
- *Picea glauca & intermed*
- *Other*

6.3.3 *Picea glauca* Series

Most of the stands in this Series were also subclimax due to past fires and were dominated by *Pinus contorta*. Relict trees from previous fires complicate the stand history, but the relatively uniform ages of *P. contorta* indicate that the most recent, and significant fire occurred in about 1905 (Table 12, p. 111), and was confined primarily to the more xeric portions of the Series. Only two stands (1, 7) were considered climax, or near-climax with *P. glauca* densities distributed throughout a wide range of size classes (see Fig. 1, p. 21 for stand locations).

P. glauca and/or intermediate spruce occurred both in the understory and as pre-fire relicts. Four h.t.s were identified for the Series with an elevation range of about 1000 to 1600 m. The h.t.s were generally more mesic than those in the *Pseudotsuga* Series, occurring primarily on alluvium near the creek, in coves between terraces or on cooler exposures (N to E), especially at the lower elevations.

Pseudotsuga menziesii was present in many of the stands and probably plays a successional role along with *Pinus contorta*. Within many of these stands, however, *P. menziesii* occupied the slightly more upland position in relation to *Picea*. *P. menziesii* often occurred as older pre-fire relicts and a complex stand history is indicated (Table 12).

6.3.3.1 *Picea glauca/Carex vaginata/Linnaea borealis* h.t.

This h.t. was limited to low alluvial terraces at Jasper Lake (1000 m elevation) and was represented by stand 1 which was well delimited

from the other stands of the Series on the ordination and cluster analysis (Figs. 8, p. 97, & 9, p. 100). The site was hydric with the ground water < 1 m below the surface of the sandy soil. The area receives some aeolian deposits from sand bars which are exposed in Jasper Lake during winter and also from the exposed limestone ridges on Gargoyle Mtn and Mt Greenock. The latter is probably the more significant material source since the prevailing wind is from the WNW. The climax association was represented with an effective stand age of 263 yrs (Table 12, p. 111). The h.t. is illustrated in Plate 4.

The tree canopy was relatively dense (h.t. mean cover = 60%) and composed mainly of *Picea glauca*, though *Alnus tenuifolia* was also present in the stratum. Tree sizes ranged up to 46 cm dbh and 27 m height. Tree density and basal area were 820 stems ha^{-1} and 19 m^2 ha^{-1} respectively. Self perpetuation of *Picea glauca* is indicated by a relatively large number of seedlings and transgressives (4080 stems ha^{-1}).

The shrub stratum was very sparse having a 7% cover. *Amelanchier alnifolia* was the most prominent with *Salix bebbiana, Rosa acicularis* and *Viburnum edule* also present (Table 11, p. 105). *Cornus stolonifera* was also found in the community but occurred in only a few of the plots and had been heavily browsed.

Although the water table was quite high, the surface soil beneath the larger trees appeared quite dry and was often floristically depauperate. The area directly beneath the trees also contained some squirrel caches

Plate 4. The mature vegetation of the *Picea glauca/Carex vaginata - Linnaea borealis* (stand 1; A) and *P. glauca/Linnaea borealis/Hylocomium splendens* (stand 7; B) h.t.s, and the seral vegetation of the *P. glauca/Elymus innovatus/Cornus canadensis* h.t.s (stand 14; C).

A

B

C

and thus the herb and low shrub species were confined primarily to the areas between crowns. *Linnaea borealis* (14%) and *Carex vaginata* (8%) characterized the herb and low shrub stratum. Minor species included *Pyrola asarifolia* and *Aster conspicuus* (Table 11, p. 105). Although *Equisetum pratense* exhibited an aspect dominance in some parts of the stand, its actual cover was quite low.

The bryophyte stratum characterized the understory having a total cover of 63% (Plate 4). *Hylocomium splendens* (50%) and *Thuidium abietinum* (10%) were by far the most dominant, with *Cladonia gracilis, C. phyllophora, Distichium capillaceum* and *Drepanocladus revolvens* having a cover of only 1% (Table 11).

6.3.3.2 *Picea glauca/Linnaea borealis/Hylocomium splendens* h.t.

Stands of *Picea glauca* with trees up to 42 m tall occurred in coves between glaciofluvial terraces, mostly on the N-facing valley slope between 1100 and 1300 m. The h.t. was composed of three stands (5, 7, 10) which along with stand 1 formed the initial group on the cluster analysis (Fig. 8, p. 97). The ordination indicated a relatively close relationship between stands 1, 7 and 10, but stand 5 appeared intermediate to *Pseudotsuga* associations (Fig. 9, p. 100), probably due to a different fire history; tree ages indicated a more recent and complete burn occurred in stand 5 (Table 12, p. 111). Stand 7, on the other hand, represented the association, being in a near-climax condition (Plate 4B). A few large *P. menziesii* and *P. contorta* still persist in it however.

The tree stratum had a cover of 55% and basal area of 38 m^2 ha^{-1} (h.t. means). Since the stand ages varied, the relative abundance of *P. glauca*, *P. menziesii* and *P. contorta* was also variable. *P. contorta* accounted for 83% of the tree cover in stand 5, whereas *P. glauca* and *P. menziesii* were disturbed throughout the range of size classes (to 69 cm dbh). *P. glauca* was especially dominant in the seedling and transgressive classes accounting for 68% of the total. Tree density averaged 2190 stems ha^{-1}.

Shrub cover was only 18% (h.t. mean) with *Juniperus communis*, *Rosa acicularis*, *Symphoricarpos albus* and *Alnus crispa* the most abundant (Table 11, p. 105). Herbs and low shrubs were more common, having a cover of 36%, with *Linnaea borealis* very conspicuous, and comprising over 25% of the total (Table 11). Minor species included *Elymus innovatus*, *Aster conspicuus*, *Cornus canadensis*, *Disporum trachycarpum* and *Pyrola virens*.

The bryophyte stratum characterized the understory (Plate 4) having a cover of 86%. Feathermosses *(Hylocomium splendens, Pleurozium schreberi)* formed a dense carpet, especially in the older stands (7, 10; Table 11). Lesser species included *Peltigera canina*, *P. aphthosa*, *Cladonia chlorophaea*, and *Cladonia* spp.

6.3.3.3 *Picea/Elymus innovatus/Cornus canadensis* h.t.

Moderate E to SE-facing colluvial slopes or gentle S-facing slopes between about 1300 and 1500 m elevation comprised this h.t. (stands 13,

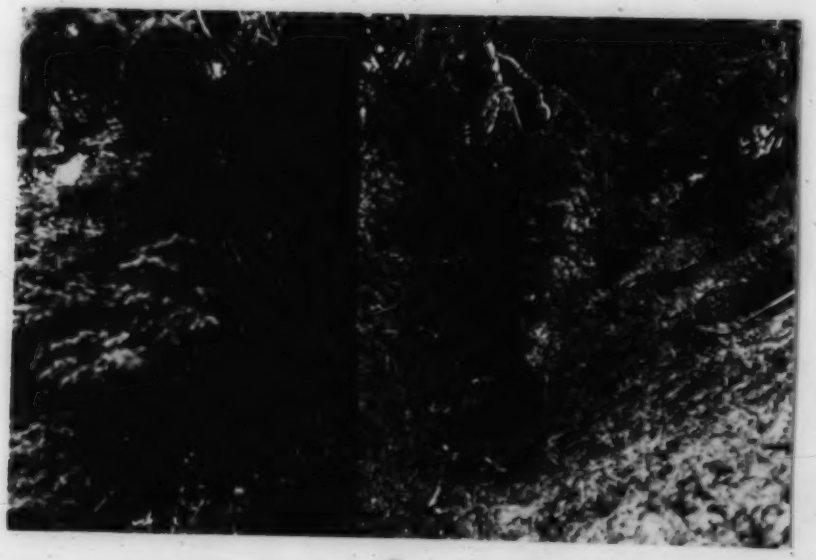
14, 18; see Fig. 1), which has a history of relatively recent fire with ESAs between 49 and 54 years (Table 12, p. 111). The h.t. occurred along the lower fringe of the subalpine forests containing *Abies lasiocarpa* and both *P. glauca* and "intermediate" spruce occurred in the understory and as pre-fire relicts. A cooler mesoclimate than the previous h.t.s of the series was indicated with more mesophytic and/or subalpine floristic elements (*Ledum groenlandicum*, *Vaccinium* spp., Table 11, p. 105). The h.t. is illustrated in Plate 4C.

Tree canopy cover was 48%, and strongly dominated by *P. contorta* (Table 11). The recentness of the burn and perhaps the slow rate of regeneration were indicated by tree size class distribution with *P. contorta* dominating size classes between sapling and about 31 cm dbh, and most of the 28 m^2 ha^{-1} basal area (see Fig. 12). However, the trend toward the association was indicated by the high proportion of *Picea* in the seedling-transgressive classes (89%), with "intermediate" spruce more abundant at the higher elevation (stand 18). Total tree (> 4 cm dbh) density was 1540 stems ha^{-1}.

The more abundant shrubs included *Shepherdia canadensis*, *Alnus crispa*, *Amelanchier alnifolia* and *Ledum groenlandicum*. The stratum was relatively open, however, with a total cover of 25%. A dense herb and low shrub stratum (cover of 56%) typified the understory with *Elymus innovatus*, *Cornus canadensis*, *Arnica cordifolia*, *Linnaea borealis* and *Aster conspicuus* the dominants (Table 11). Other less constant, but sometimes abundant species included *Lathyrus ochroleucus*, *Pyrola secunda*, *Achillea millefolium* and *Clematis verticellaris*.

Plate 5. The *Picea/Alnus crispa/Elymus innovatus* (stand 20; A) and *Picea - Pinus albicaulis/Juniperus communis/Elymus innovatus* (stand 29; B) h.t.s of the *Picea glauca* series.

A



B

The bryophyte stratum (cover of 54%) consisted almost entirely of feathermosses *(Hylocomium splendens, Pleurozium schreberi, Ptilium crista - castrensis)*, with only a few lichens *(Cladonia gracilis, C. cornuta, Alectoria glabra)* represented (Table 11, p. 105).

6.3.3.4 *Picea/Alnus crispa/Elymus innovatus* h.t.

Three stands (16, 19, 20) comprised the h.t. which occurred on the steep portion of the constant slope between about 1400 and 1570 m elevation. As with the *Pg/Ei/Cc* h.t., the stands were elevationally adjacent to the subalpine *Picea-Abies* forest and "intermediate" spruce was indicated as the potential climax species (Table 10, p. 87; Plate 5A).

The stands were closely positioned to each other on the montane ordination (Fig. 10), and 16 and 19 were shown as being closely related on the ordination of all stands and also formed part of cluster IX (Fig. 8).

The h.t. was quite similar in topographic position and fire history to the *P/Ei/Cc* h.t. (Table 12). The *P/Alc/Ei* h.t. is, however, the more mesic, occurring at slightly higher elevations, often on E to NE-facing slopes (Table 11, p. 105).

The tree stratum was dominated by *P. contorta* which accounted for 81% of the total tree cover (51%) and also most of the 24 m^2 ha^{-1} basal area. Intermediate spruce was dominant only in the seedling and transgressive size classes and occurred as scattered pre-fire relicts > 23 cm

dbh. Total tree density was 14,450 stems ha^{-1}, much higher than in *Pg/Ei/Cc*.

Shrubs were a prominent component of the community having a cover of 40%. Dominant species included *Alnus crispa, Rosa acicularis, Shepherdia canadensis* and *Salix bebbiana*. *Menziesia glabella, Vaccinium membranaceum, Juniperus communis* and *Amelanchier alnifolia* occurred sporadically through the h.t. (Table 11, p. 105).

Herbs and low shrubs were relatively abundant with a 44% cover for the stratum. *Elymus innovatus, Cornus canadensis, Linnaea borealis* and *Arnica cordifolia* where dominant with *Pyrola virens, Aster ciliolatus, A. conspicuus, Epilobium angustifolium* and *Clematis verticellaris* and *Aster conspicuus* in a minor role (Table 11, p. 105). The bryophyte stratum was relatively sparse having a cover of 22%; *Hylocomium splendens* was by far the most prominent with *Pleurozium schreberi, Cladonia gracilis, C. ecmocyna,* and *Alectoria glabra* much less so.

6.3.3.5 *Picea-Pinus albicaulis/Juniperus communis/Elymus innovatus* h.t.

Communities on steep S to SW-facing slopes and ridge-tops between about 1700 and 1900 m elevation occupied this h.t. (Plate 5B). Data from two stands (29, 32) were used to characterize the association. The h.t. occurred above much of the *Picea-Abies* forest and thus forms a distinctive band on xeric, wind-exposed ridges on rocky soil. The two stands have a complex fire history, with *Pinus contorta* and *Pseudotsuga menziesii* present as seral species. The *P. contorta* population had a

mean age of 60 years at the lower stand where the last major fire occurred about 1910. Several relatively old *Pinus albicaulis*, *P. contorta* and *Pseudotsuga menziesii* occurred in both stands (Table 12, p. 111).

The h.t. appears as a distinct group on the ordination (Fig. 9) and along with a number of other stands, forms cluster VI on the cluster analysis (Fig. 8, p. 97). The stands of the h.t. were intermediate to those of the *Pseudotsuga* and *Picea* Series on the ordination and on the cluster analysis, but were delimited as a unit by both methods.

The tree stratum had a cover of 54% and was composed mostly of "intermediate" and Engelman spruce, *P. contorta* and *P. albicaulis* (Table 11). Basal area was 25 m^2 ha^{-1} with 51% accounted for by *Picea*. Tree density was 3260 stems ha^{-1} with *P. menziesii* and *Picea* extending to 46 cm dbh in size.

Juniperus communis and *Shepherdia canadensis* were the dominant shrubs, and reproduction of the tree species formed the rest of the sparse stratum (Table 11, p. 105). The herb and low shrub layer was relatively open (24% cover) and was composed mainly of *Elymus innovatus*, *Linnaea borealis* and *Arnica cordifolia* (Plate 5). Minor species of the stratum included *Galium boreale*, *Pyrola virens*, *P. secunda*, *Epilobium angustifolium* and *Achillea millefolium* (Table 11). The open understory was also emphasized by a sparse bryoid layer (7% cover), with *Hylocomium splendens*, *Ptilium crista-castrensis* and *Icmadophila ericetorum* the most notable (Table 11).

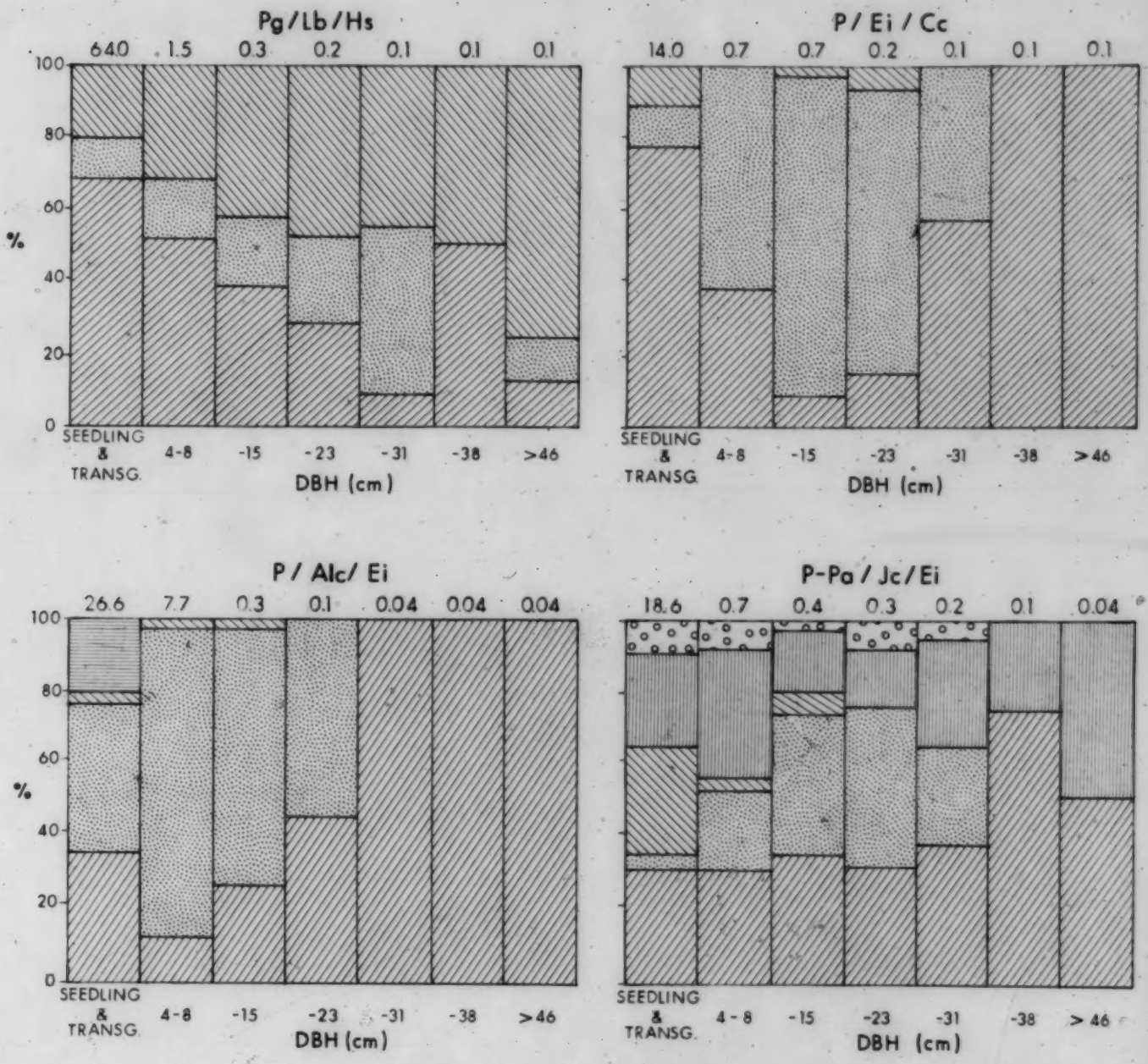
6.3.3.6 Size distribution of trees in the *Picea glauca* Series

Picea glauca was evenly distributed through the range of size classes in the *Pg/Cv-Lb* h.t. with no other tree species present. *P. glauca* also occurred throughout the range of size classes of the *Pg/Lb/Hs* h.t., but the subclimax character of some stands was evident in the high proportion of *Pinus contorta*, and possibly *Pseudotsuga menziesii* in the larger sizes (Fig. 12). The latter species was most prominent as large, widely spaced pre-fire relicts. The occurrence of *P. contorta* in the 15 to 31 cm dbh classes in Figure 12 is due mainly to the influence of the younger stands.

Histograms of the *P/Ei/Cc* and *P/Alc/Ei* h.t.s show a successional trend with *Picea* dominating the small size classes and *P. contorta* the larger (Fig. 12). *Picea* also occurred in the larger size classes and this is due partially to pre-fire relicts, but *Picea* may have regenerated at about the same time as *P. contorta* following fire.

The *P-Pa/Jc/Ei* h.t. appeared to be unique with a number of species occurring through much of the range of size classes (Fig. 12). *P. menziesii* occurred only in a few of the smaller size classes. *P. contorta* on the other hand, occurred primarily as large scattered individuals and both species were more prominent at the lower elevation of the h.t., probably originating after a relatively old fire as ages were centered around 100 yrs. However, a complex fire history was indicated for the h.t. (see Table 12, p. 111). *Picea* and *P. albicaulis* occurred mostly in the smaller size classes and are postulated to co-dominate the association. Development toward a climax community appeared

Figure 12. Histograms showing the size class distribution of major tree species in the *Picea glauca* Series. Although *P. glauca*, "intermediate spruce" and *P. engelmannii* all were present in the series, *P. glauca* was the most prominent. Tree density (stems ha^{-1} X 100) is given above each category.



TREE SPECIES LEGEND

- *Picea (glauca, intermediate, engelmannii)*
- *Pinus albicaulis*
- *Pinus contorta*
- *Abies lasiocarpa*
- *Pseudotsuga menziesii*
- *Other*

to have been relatively slow, due possibly to the xeric nature of the h.t., the rocky soils and the reduced ability of *P. contorta* to reforest high elevation area after fire.

6.3.4 *Picea engelmannii - Abies lasiocarpa* Series

A large portion of the drainage basin contained a relatively homogeneous forest which typifies the subalpine zone. The Series is easily recognized by the co-dominance of *Picea engelmannii* and *Abies lasiocarpa*, but the absolute and relative abundances of the two species varied considerably.

Elevational range was from about 1600 to 2400 m with most of the forest confined to constant colluvial slopes. The forest also extended onto alluvial terraces and the adjacent constant concave slope, but both landforms were limited in areas. Some trees extended into the avalanche chutes and cirques, forming an ecotone between subalpine forest and meadow.

Pinus contorta appeared as a successional species in a burned section along the lower elevational limit of the series (adjoining *P/Ei/Cc & P/Ac/Ei* h.t.s) and occasionally in other h.t.s. *Pinus albicaulis* appeared as an associate of h.t.s on steep SW-facing slopes. *Picea mariana* occurred as a minor species in a number of stands, mostly on the moist, gentler waxing slopes near the valley floor. The Series was composed of three h.t.s, most of which contained relatively mature communities, representing the associations.

The h.t.s were quite distinct as stand groups on the ordination (Fig. 9, p. 100), and also in the cluster analysis, although groups in the latter also contained some montane stands and the subalpine stands were not depicted as being so contiguous (Fig. 8, p. 97).

6.3.4.1 *Picea engelmannii - Abies lasiocarpa/Menziesia glabella - Vaccinium membranaceum* h.t. -

A relatively large portion of the Series was characterized by a *Menziesia - Vaccinium* shrub union which occurred predominantly on the lower, gentler and moister portions of the constant slope (1500 - 1680 m). The h.t. is illustrated in Plate 6A & B. Aspect was mostly W or SW although areas of both valley slopes were represented (Table 11, p. 105).

Much of the h.t. was occupied by the climax and contained *Picea* and *Abies* as the dominant trees throughout the size class range (see Appendix 2). Populations of *Picea engelmannii* were predominant with only stands 21, 22 and 23 having MI's below 300, i.e. intermediate spruce (Table 10, p. 87).

A visually evident fire margin was located at the lower elevation limit of the h.t. between 1500 and 1600 m elevation (see Plate 1, p. 46); stands 21 and 22 occurred in the burn area and thus represented seral vegetation. Significant changes in composition and in moss cover, were associated with the fire, such that the climax and preclimax stands were widely separated on the cluster analysis (stands 23, 24, 25 and 27

Plate 6. The *Picea engelmannii - Abies lasiocarpa* Series. Photos A and B respectively illustrate seral and mature vegetation of the *P. engelmannii - A. lasiocarpa/ Menziesia glabella - Vaccinium membranaceum* h.t. *Picea - Abies/Arnica cordifolia* and *Picea - Abies/Arnica divercifolia/Hylocomium splendens* h.t.s (stand 30; C) (stand 33; D) are of climax vegetation. Note aspect dominance of *Equisetum pratense* in C.

A

C

D

in cluster II; and stands 21 and 22 in cluster X, Fig. 8). However, the same degree of separation was not made on the ordination (Fig. 9, p. 100). Some floristic differences may result from elevational differences since the more mature vegetation occurred at a higher position on the slope (1615 - 1680 m). Stands 22 and 23 were in close proximity with only a 5 m elevational difference and were treated as burn and control areas respectively for making comparisons on seral and climax portions of the h.t. Thus all the stands were postulated as belonging to a single h.t. with understory differences accounted for by stand age disparity. The seral and mature portions are characterized below.

6.3.4.1.1 Seral Communities of *Pe-Al/Mg/Vm* h.t.

Communities of the burned area had ESAs of about 50 years (stands 21, 22; Table 12, p. 111). As with some of the *Picea* h.t.s, tree age data indicated a major fire between 60 and 65 years ago (1910-1915). This would be the most recent period of significant fire within the subalpine forest zone. The fires were confined mostly to the lower and central area of the basin, however. There is also the possibility, as mentioned previously, that the rate of regeneration of *Pinus contorta* after fire was slower here than at the lower elevations. Relict intermediate spruce and *P. contorta* contained a number of burn scars indicating more than one fire. Most of the *Picea* regeneration appeared to have begun about 15 years after *P. contorta* establishment on S exposed slopes, whereas N exposed slopes of the area had a wider range of tree ages.

Community structure was characterized by a fairly open tree stratum with a heavy understory of shrubs and some fallen trees (Plate 6A). *P. contorta* dominated the tree stratum, comprising 52% of the 34% total mean cover, and "intermediate spruce" was much less abundant. *Picea mariana* and *Abies lasiocarpa* were minor components of the tree stratum with less than 2% mean cover (Table 11, p. 105). *P. contorta* dominance was also illustrated by population size distribution with high densities in all categories (seedling to 31 cm dbh). Average tree density was 1923 stems ha^{-1} with most of the population between 4 and 8 cm dbh. Tree seedling density was relatively high and was composed mostly of *P. glauca* x *engelmannii* and *A. lasiocarpa*. Mean basal area was 16 m^2 ha^{-1}, with *P. contorta* and *P. glauca* x *engelmannii* being the most abundant components.

The shrub stratum was a very prominent feature of the seral community having a mean cover of 63%. Most of this was contributed by *Menziesia glabella*, but *Ledum groenlandicum* and *Vaccinium membranaceum* were also abundant (Table 11). Other important species included *Shepherdia canadensis*, *Ribes lacustre* and seedlings and transgressives of intermediate spruce and *A. lasiocarpa*.

Mean cover of the herb and low shrub stratum was 35% with *Cornus canadensis*, *Elymus innovatus*, *Equisetum scirpoides* and *Vaccinium scoparium* the major species (Table 11). The bryoid stratum was relatively rich in species, but had a mean cover of only 28% for both stands. Major species included *Hylocomium splendens*, *Pohlia nutans* (in stand

22), *Drepanocladus uncinatus*, *D. revolvens* (in stand 21) and a number of lichen species (including *Cladonia gracilis*, *C. phyllophora*, *Peltigera aphthosa* and *Usnea scabrata* ssp. *nylanderiana*).

6.3.4.1.2 Climax Communities of the *Pe-Al/Mg-Vm* h.t.

The more mature portion of the h.t. (stands 23, 24, 25 and 27) was characterized by the *Picea - Abies* union which occurred throughout the range of tree sizes.

ESA ranged from 195 to 236 years (Table 11, p. 111). The *Picea engelmannii* populations usually had older and larger trees than those of *Abies lasiocarpa*, probably due to genetic (i.e. life-span), not historic factors.

The tree stratum had an average cover of 51% for the four stands with *Picea* having the highest proportion (Table 11, p. 105). Total tree density was quite high with a mean of 2095 stems ha^{-1} for the four stands. *P. mariana* was also relatively abundant in the smaller size classes. Total basal area averaged 21 m^2 ha^{-1} with large *P. engelmannii* trees (to 69 cm dbh) an important part of the total. Regeneration of *P. engelmannii* and *A. lasiocarpa* was a significant component of the lower strata with seedling and transgressive categories containing 34,600 stems ha^{-1}.

As in the burned area, the shrub layer was a prominent feature of the community, but was not as dense nor as consistent throughout the stands (Plate 6). Average shrub cover was 28% for the h.t. with *Menziesia glabella, Vaccinium membranaceum* and *Rhododendron albiflorum* the most dominant species (Table 11, p. 105). Less important species included reproduction of the dominant trees and *Shepherdia canadensis*.

Linnaea borealis, Arnica cordifolia and *Cornus canadensis* were the principal species within the herb and low shrub stratum which had an average h.t. cover of 12% and was fairly sparse (Plate 6). More minor species included *Vaccinium scoparium, V. caespitosum, Pyrola secunda* and *Elymus innovatus* (Table 11). The bryoid component of the ground vegetation was very prominent having a mean cover of 95%. *Hylocomium splendens* was the most abundant species with *Pleurozium schreberi, Ptilium crista-castrensis* and *Usnea scabrata* spp. *nylanderiana* more secondary. Other prominent species included *Aulocomnium palustre, Plaziomnium cuspidatum* and *Cladonia fimbriata* (Table 11).

Quantitatively, some important species were differentially distributed among the stands indicating site variability within the h.t. *Shepherdia canadensis* and *Juniperus communis* were much more abundant at lower elevations (stands 24, 25) and occurred in openings in the canopy due mainly to windthrow. Understory species, more prominent in the lower elevation stands included *Pyrola secunda, Cladina mitis* and *Peltigera aphthosa*, whereas *Lycopodium annotinum, Aulacomnium palustre* and *Cladonia fimbriata* were more abundant at the higher elevations. However, the

majority of the species appeared throughout the stands and thus the cluster and ordination unity.

6.3.4.1.3 Floristic Differences Between Seral and Mature Communities of the *Pe-Al/Mg-Vm* h.t.

A comparison of the flora in stands 21 and 22 with that of 23 was used as a guide for ascertaining changes in the h.t. due to fire, and to assess the rate of change toward the association. The tree stratum differed sharply, with no *Pinus contorta* appearing in the mature stand. Understory species more abundant in, or restricted to seral stands 21 and 22 included *Ribes lacustre, Ledum groenlandicum, Elymus innovatus, Cornus canadensis, Equisetum scirpoides, Cladonia phyllophora* and *C. gracilis* (Table 11, p. 105). Few species were restricted to the unburned area, and instead an increase in the mean cover of *Rhododendron albiflorum, Hylocomnium splendens, Pleurozium schreberi, Ptilium crista-castrensis, Dicranum polysetum* and *Distichium capillaceum* appeared to distinguish vegetation maturity. Since the understory species were fairly continuous between the stands, it is postulated that the recovery rate of the lower strata is more rapid than and not necessarily dependent on the tree stratum. A number of shrubs *(Menziesia glabella, Vaccinium membranaceum* and *Rhododendron albiflorum)* probably regenerate from root stocks, unless the fire is severe, and thus provide the necessary shade for the return of other climax ground cover species. A reduction from 35 to 29 species was found between seral and the more mature stands.

6.3.4.2 *Picea engelmannii - Abies lasiocarpa/Arnica cordifolia* h.t.

The abundance of *Arnica cordifolia* and mosses was primarily responsible for the combination of stands 28 and 30 into Cluster II, and their separation from other stands in the series on the ordination Figs. 8, p. 97 & 9, p. 100). The h.t. was located on the lower portion of the constant slope and on the concave slope adjacent to the valley floor near the head of the drainage basin on both the SSW and NE exposures of the valley slope. Elevation ranged from about 1700 to 1750 m.

The h.t. contained mature vegetation with *Picea engelmannii* the dominant tree. Mean ESA was 201 years with *P. engelmannii* having the oldest and largest trees (up to 84 cm dbh and 30 m tall) (Table 12, p. 111). Tree canopy cover averaged 53% most of which was of *P. engelmannii*, but *A. lasiocarpa* contributed nearly 50% of the total in stand 30 (Table 11, p. 105). *P. mariana* cover was not higher than 1%. Mean basal area was 30 m^2 ha^{-1} and composed mostly of *P. engelmannii*, although *A. lasiocarpa* was quite important in stand 30. Average tree density was 4470 stems ha^{-1}, with the seedling class of *A. lasiocarpa* containing the majority (Appendix 2).

The shrub stratum was physiognomically not a prominent feature of the h.t. even though the mean cover averaged 39%, due to the luxuriant nature of the understory (Plate 6). Seedlings and transgressives of *A. lasiocarpa* were the dominant species and *Menziesia glabella* and *Rhododendron albiflorum* more prominent on the steeper areas (stand 30). *Salix glauca* and *Vaccinium membranaceum* were also dispersed contagiously (Table 11).

Average herb and low shrub cover was 33% with *Arnica cordifolia, Cornus canadensis, Pyrola secunda* being the most abundant. Other major species included *Lycopodium annotinum* and *Equisetum scirpoides*. *E. arvense* formed a local aspect dominant under the larger wide-spread trees on the lower more gentle concave portion of the slope and had a mean cover of 5% (Plate 6C).

Mosses and lichens were the dominant feature of the forest floor having a mean cover of 100% for the h.t. Important species included *Hylocomium splendens, Pleurozium schreberi, Ptilium crista-castrensis, Cladonia ecmocyna* and *Peltigera aphthosa* (Table 11, p. 105). A number of *Cladonia* spp. were a common feature of the h.t. but individually exhibited low cover.

Vegetation on the NE exposed slope may have developed at a faster rate than that facing toward the SW which had an older ESA (stand 28, Table 12). *A. lasiocarpa* appears to have originated sooner after *P. engelmannii* on the NE-facing slopes with mean and maximum ages closer to those of spruce.

The shrub stratum was more pronounced in stand 30, but except for the presence of *Salix glauca*, there was little difference in composition between the two sites (Table 11, p. 105). Variance within the lower stratum was also not pronounced, but *Linnaea borealis* and *Elymus innovatus* were more abundant on the SW exposure. Although some dissimilarities appeared between the two sites, the more mesic condition of a NE exposure

may be compensated for by an increase in slope steepness and thus a single h.t. was represented.

6.3.4.3 *Picea engelmannii - Abies lasiocarpa/Arnica diversifolia/Hylocomium splendens* h.t.

Communities near the upper elevational limit of forest occurred on the h.t. which was represented by stands 31 and 33. The stands were delimited from the rest of the vegetation on the cluster diagram and the ordination, although not as distinctly by the latter (Figs. 8, p. 97 & 9, p. 100). Both sides of the valley were included, with SW and NE exposures. The h.t. occurs on the upper constant colluvial slope and ranges in elevation from 1840 to 2040 m (Table 11, p. 105).

Pinus albicaulis and "intermediate spruce" (MI of 218, Table 10) characterize the lower, more xeric SW-exposed sites.

The tree stratum had a mean cover of 56%, basal area of 13 m^2 ha^{-1} and density of 3260 stems ha^{-1}. Large trees (-46 cm dbh), mostly of *P. engelmannii*, were more common in stand 31, whereas smaller size classes and high density typified the sites at the higher elevation (stand 33, Plate 6D). The shrub stratum was relatively sparse (cover = 4%), and dominated by *Salix barratiana* and seedlings and transgressives of *A. lasiocarpa* (Table 11, p. 105).

Herbs and low shrubs were more prominent, forming a luxuriant understory especially at the higher elevations (Plate 6D). Average

cover for the stratum was 17% with *Arnica diversifolia*, *Pyrola secunda* and *Fragaria virginiana* the most constant, abundant species (Table 11, p. 105). The latter species occurred primarily in the more open areas. Bryophytes and lichens were also an important part of the understory having a mean cover of 29%. Major species included *Hylocomium splendens*, *Pleurozium schreberi*, *Peltigera aphthosa* and *Cladonia ecmocyna*.

Compositional differences between the two sites were evident in the subordinate and tree strata. Stand 31, with a SW exposure, was recognized as being more xeric and contained *Rosa acicularis*, *Cornus canadensis*, *Arctostaphylos uva-ursi*, *Dicranum polysetum*, *Distichium capillaceum* and *Plaziomnium cuspidatum*. *Salix barratiana*, *Pyrola minor*, *Phyllodoce empetriformis*, *Lycopodium annotinum*, *Barbilophozia lycopodioides*, *B. hatcheri*, *Drepanocladus unciniatus* and *D. revolvens* were restricted to the higher elevation on NE exposures (Table 11, p. 105).

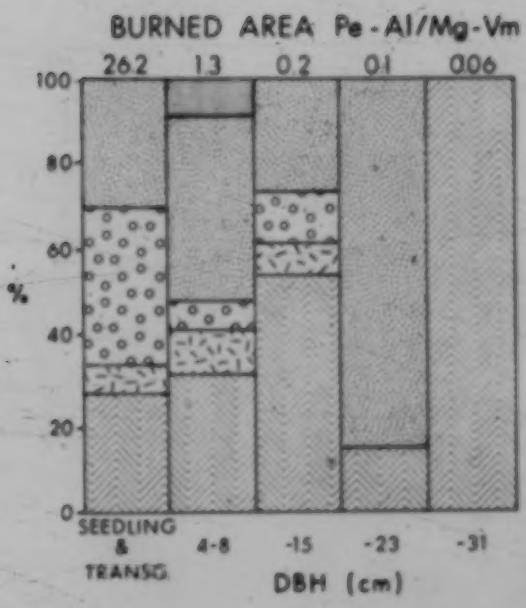
The pathway to a climax condition may have varied between the two stands, with the more xeric area lagging behind in development and including a *Pinus albicaulis* element. The areas on the SW-facing slopes are postulated as eventually developing into the same association as these on NE-facing slopes, but the rate of change on the former has probably been retarded by rugged topography and a thin Lithic Regosol. It is recognized that two topoedaphic climaxes may be included in the h.t., but, enough understory species were common to both stands to give recognizable cluster and ordination affinities, and thus the h.t. was left intact.

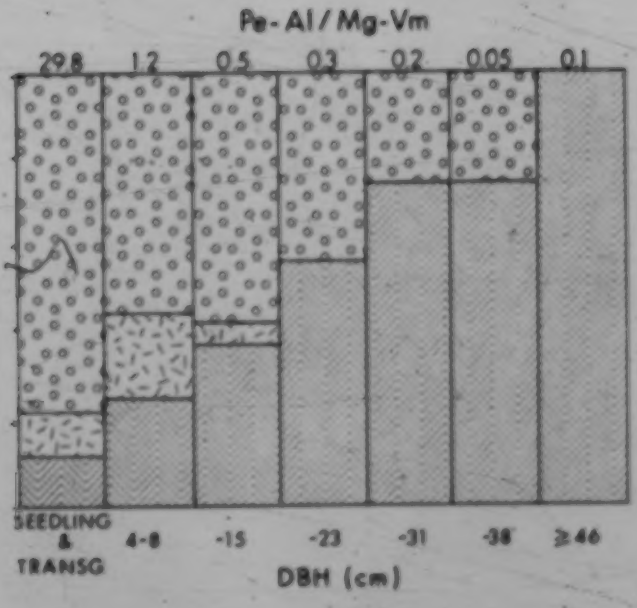
6.3.4.4 Tree Species Size Distribution

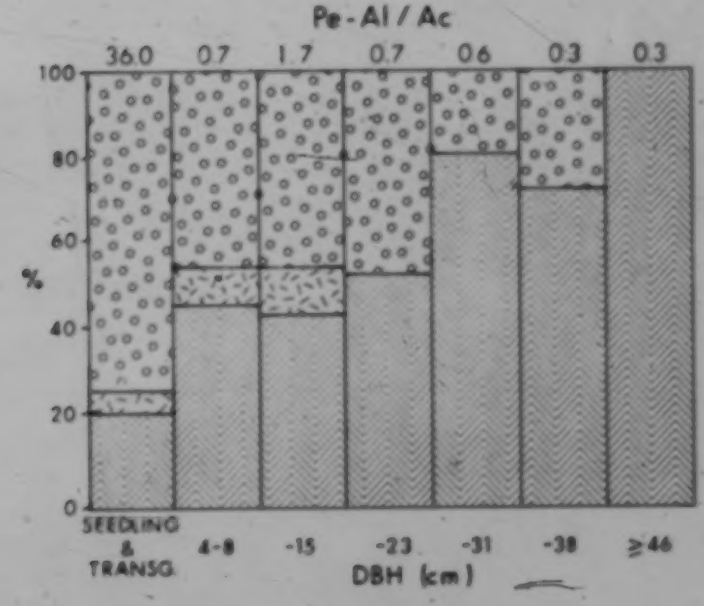
The compositional difference between the association and subclimax portions of the *Pe-Al/Mg-Vm* h.t. was quite apparent when plotting the size class distribution of the tree species (Fig. 13). *Pinus contorta* was especially dominant in the larger size classes (15-23 cm dbh) and also appeared as seedlings and saplings in the burned area. *P. contorta* was, however, only a trivial component of the more mature community. Examination of the lower size class densities indicated an apparent potential for *A. lasiocarpa* to increase. *P. engelmannii*, though of lower density may persist because of its lower mortality rate. *A. lasiocarpa* had a much higher dead to live total stem ratio (1:27 vs. 1:37 for *P. engelmannii*). *P. engelmannii* occurred in a wider range of size classes than *A. lasiocarpa* and was also the older of the two in all h.t.s. Distributional characteristics of the two species were quite similar for the *Pe-Al/Mg-Vm* and *Pe-Al/Ac* associations (Fig. 13). *P. mariana* was a minor component in both h.t.s and was confined to the smaller size classes.

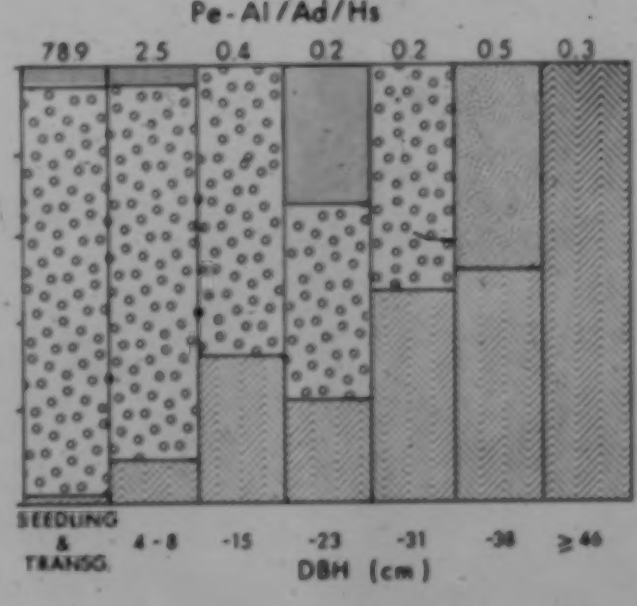
The reproductive potential of *A. lasiocarpa* appeared to be very high for the *Pe-Al/Ad/Hs* h.t. However, this is critically offset by a high mortality with a 500:1 dead to live ratio exhibited by tallying both the densities of the seedling and transgressive size classes. Almost all of the *A. lasiocarpa* in the transgressive class were dead. However, the tendency of *A. lasiocarpa* to increase in dominance was more apparent in this h.t. than in the others and *P. engelmannii* was quite uncommon in the smaller size classes (Fig. 13). This relationship

Figure 13. Histograms showing the size class distribution of tree species in the *Picea engelmannii - Abies lasiocarpa* Series. Size distributions of the burned and unburned portions of the *Pe-Al/Mg-Vm* h.t. are shown separately. Tree density (stems ha^{-1} X 100) is given above each category.









TREE SPECIES LEGEND

- *Picea engelmannii*
- *P. mariana*
- *Abies lasiocarpa*
- *Pinus contorta*
- *Other*

between the two conifer species in the *Pe-Al/Ad/He* h.t. may reflect the ability of *A. lasiocarpa* to reproduce by layering at the higher elevations of the basin.

6.3.5 Subalpine Meadow and Scrubland Series

Subalpine meadow and scrub communities were quite disjunct, being restricted mainly to fossil tarns at the head of the valley and to cirques near the Gargoyle Mtn headwall. Two h.t.s were recognized with climax meadow and shrub vegetation representing these respectively. Physiognomy appeared as a function of elevation. Scrubland vegetation was predominant in the area near the head of the valley floor at 1670 m, and meadow was more extensive in the cirques at about 2000 m.

P. engelmannii occurred sporadically as small trees throughout the series, but its standing dead attest to a marginal and fluctuating environment for tree establishment. Browsing and grazing evidence occurred in all stands and may be a factor in preserving their present structure and composition. The series was composed of the most species-rich stands of the drainage basin, was represented by Cluster VIII and was also quite distinct on the ordination (stands 26, 34, 35; Figs. 8, p. 97, & 9, p. 100).

6.3.5.1 *Salix glauca/Elymus innovatus* community

The community was characterized by moderately tall shrubs ($\geq$ 1 m) with a dense herb understory, and was best developed on a fossil lake bed at the head of the valley (stand 26). Thus the community occurred

as an island within the *P. engelmannii - A. lasiocarpa/Menziesia glabella - Vaccinium membranaceum* association which occupied the adjacent slopes (Plate 7).

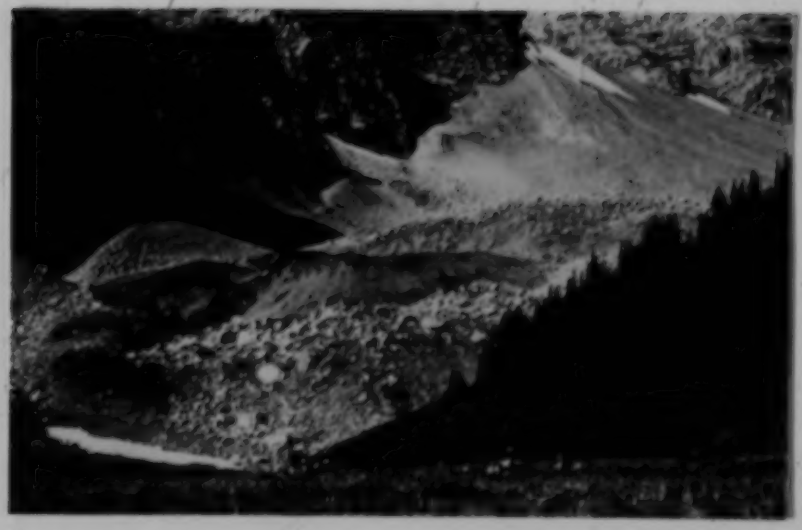
The shrub synusium had a mean cover of 18% and was quite variable in distribution. Dominance was shared by *Salix glauca* and *Betula pumila glandulifera*. Other relatively abundant species included *Potentilla fruticosa, Salix barratiana* and seedlings and transgressives of *P. engelmannii*, all of which had mean cover of less than 1% (Table 11, p. 105).

The herb and low shrub stratum had a mean cover of 54% and was a dominant feature of the community although the shrubs were more striking physiognomically (Plate 7). Dominants included *Elymus innovatus, Danthonia intermedia, Carex media, Delphinium glaucum, Arctostaphylos rubra* and *Pedicularis bracteosa* (Table 11). Bryoid cryptogam cover averaged 14% and consisted mostly of *Sphagnum warnstorfii*.

The community was postulated as representing an edaphic climax occurring only on cold, wet, silty soils of lacustrine origin. *P. engelmannii* occurred as widely scattered and various sized individuals with some standing dead. Thus the area appeared to be only marginally suitable for tree growth, with establishment probably occurring more readily during relatively dry periods. *Salix glauca* has been heavily browsed by moose and a number of animal trails dissected the area. Browsing may favor the herbaceous understory species as the potential

Plate 7. Subalpine shrub meadow series illustrating the *Salix glauca/Elymus innovatus* (stand 26; A) and *Salix vestita/Poa alpina* (stand 35; B) h.t.s.

A



shrub cover is not realized. However, the zootic influence was postulated as secondary to edaphic factors in influencing the community since the shrub cover was relatively high. Permafrost occurred sporadically in this community, and was confined mostly to hummocks beneath willow. No other permafrost was found in the drainage basin.

6.3.5.2 *Salix vestita/Poa alpina* community

The basins of glacial cirques containing fossil beds or fluvial deposits that support low shrub meadow vegetation support a lush meadow community (Plate 7). The h.t. occurred primarily at about 2000 m elevation within the *Picea - Abies* subalpine forest, but stand 34 was slightly lower and had more microrelief than stand 35.

Low herbs and shrubs formed a dense plant cover that averaged 82% for the h.t. The more abundant low shrubs included *Salix barratiana, S. pseudomonticola* and *S. glauca* which had a prostrate or decumbent growth-form. The herb component was diverse and contained a number of graminoid species as dominants. *Poa alpina, Festuca brachyophylla, Phleum alpinum, Carex nigricans; C. atrosquama, Artemisia norvegica* and *Equisetum arvense* all had mean cover $\geq$ 4% (Table 11). The bryoid layer had a mean cover of 22% and was composed mainly of *Dicranum polysetum, Distichium capillaceum, Bryum* sp., *Sphagnum warnstorfii* and *Stereocaulon tomentosum.*

Although many of the species were common throughout the community, some segregation was present indicating environmental differences between the two stands. Stand 34 had more micro-relief. Species

associated with this area included *Deschampsia caespitosa, Festuca brachyophylla, Dryas hookeriana, Stereocaulon tomentosum* all of which occurred primarily on the more xeric terraces between streams, and also *Equisetum arvense, Petasites sagittatus* and *Bryum* sp. which occurred in wet areas. Drainage through stand 35 was more diffuse and impeded, occurring across much of the fossil lake basin. *Poa pratensis, Juncus drummondii, Luzula parviflora, Plantago major* and *Pohlia nutans* were more endemic to this area.

Bighorn sheep and elk were observed grazing the h.t. and have developed some trails across the cirques. Marmots inhabited the rockier surrounding moraine where their burrows were marked by the occurrence of *Veratrum eschscholtzii, Epilobium latifolium* and *Solidago multiradiata.*

6.3.6 Alpine Tundra Series

Alpine tundra, dominated by vasculars, occurred primarily on the rounded spurs and ridges near Gargoyle and Redan Mtns, sporadically on the S exposures of Roche de Smet, and was not well developed above about 2500 m on both valley slopes. Such vegetation was restricted to sites on which some soil has developed. Elsewhere, above timber-line, rock barrens and lichen tundra predominated. Rock stripes and some solifluction lobes were common to the area. The Series was represented by numerous plant communities and is characterized by general descriptions of only the more widespread types.

6.3.6.1 *Dryas hookeriana - Oxytropis podocarpa* community

Dwarf shrub, herb and grass species comprised this most common representative of alpine tundra. The association was characterized by a *Dryas hookeriana* and *Oxytropis podocarpa* union. Other major herb and low shrub species included *Arctostaphylos uva-ursi, Valeriana septentrionalis, Trisetum spicatum, Solidago multiradiata, Anemone drummondii, Carex nardina* and *Gentianella propinqua*. Prostrate shrubs of *Salix arctica* were important as an aspect dominant but had a mean cover of only 1%. Mean total cover of the herb and low shrub stratum was near 100%, and thus the turfy appearance. Bryoids were not as abundant having a mean cover of 14%, most of which was lichen. The major species included *Cetraria nivalis, Cladonia gonecha, Stereocaulon tomentosum, Plaziomnium cuspidatum* and *Tortula norvegica*.

The h.t. was more xeric than the subalpine meadow series having a coarse substratum and occurring on slopes and ridges which were exposed to wind. The greater abundance of lichens in relation to mosses is probably a reflection of the more extreme environment. Bighorn sheep and mountain goat have increased the micro-relief of the h.t. by excavating bedding hollows and have formed a series of trails along the ridges to rock outcrops and cliffs. This h.t. and other more scattered alpine communities which were not sampled appeared to be an important source of food for mountain goat.

6.3.6.2 Rock and Lichen Tundra h.t.

Much of the area near the Roche de Smet ridge above about 2300 m was quite barren. Vegetation was primarily confined to areas protected from wind and colluvial movement and deposition. The distribution of species was related to elevation and microenvironment with some mesophytic species (*Saxifraga* spp., *Telesonix heucheuriformis*, *Oxyria digyna*, *Cystopteris fragilis*, *Bryum* spp.) occurring in rock crevases. However, most of the area appeared to be quite xeric and barren. *Trisetum spicatum*, *Dryas hookeriana*, *Saxifraga oppositifolia*, *Festuca brachyphylla* and a number of lichens (*Thamnolia*, *Cetraria* spp.) were the most common species. A small flat area on Roche de Smet contained relatively well developed grassland tundra. The community bore a resemblance to the alpi[illegible]*ryas* - *Oxytropis* h.t. on the other side of the basin, but contained a much higher abundance of *Trisetum spicatum* and *Festuca brachyphylla*.

6.3.7 Other Plant Communities

Several distinctive plant community types were relatively rare components of the vegetation of the drainage basin and thus qualitatively sampled due to time restrictions. However these types can be considered an important part of the total vegetation mosaic and some are described here on the basis of their major species.

6.3.7.1 *Populus tremuloides* communities

Alluvial fans near the mouth of Vine Creek and alluvial deposits at the base of some secondary creeks contained *Populus tremuloides* communities. The vegetation near the mouth of the creek (1070 m) contained an open tree stratum that also had *Picea glauca* in the slight depressions and *Populus balsamifera* nearer the existing creek bed. The area had been disturbed by roads leading to the Snaring railroad station and by a gravel pit. Cobbles and boulders were exposed near the ground surface indicating a coarse, immature soil. Shrubs common especially under trees, included *Shepherdia canadensis, Juniperus communis* and *Rosa acicularis*. The ground cover was composed mainly of *Arctostaphylos uva-ursi, Achillea millefolium, Antennaria nitida* and *Koeleria cristata*. *Agropyron riparium, Linum lewisii* and *Solidago decumbens* were also prominent, mostly on disturbed areas.

P. tremuloides also occurred in nearly pure, dense stands on the constant slope where secondary streams have deposited relatively fine material over cobbles (1400 m; see Plate 1, p. 46). Species composition and structure of this community indicate a more mesic habitat than that on the alluvial fan. The understory appeared quite luxuriant with *Elymus innovatus, Linnaea borealis, Disporum trachycarpum, Cornus canadensis* and *Aster conspicuous* the most prominent species. Shrubs including *Rosa acicularis* and *Viburnum edule* were less abundant, occurring in the more open areas. *Picea glauca* seedlings and transgressives were common in the understory and an affinity of the vegetation with the nearby *Picea glauca/Linnaea borealis - Elymus innovatus* h.t. is indicated.

6.3.7.2 *Picea mariana* fen community

A slump near the top of the constant waxing slope at about 1450 m elevation contained a unique drainage basin h.t. (see Plate 1, p. 46). Ground water and surface drainage collects on the relatively level area and was evident as small shallow pools. Open grown *P. mariana* and dense mounds of *Sphagnum warnstorfii* characterize the community. Other more abundant species included *Betula glandulosa, Ledum groenlandicum, Carex aquatilis, Parnassia fimbriata* and *Equisetum scirpoides. Pinguicula vulgaris, Eriophorum brachyantherum, Vaccinium vitis-idaea* and *Sphagnum warnstorfii* were evaluated as the diagnostic species characterizing the fen habitat, although they were not always the most abundant. Major bryoids other than *Sphagnum* included *Dicranum polysetum, Pohlia nutans* and *Cladonia cristatella*. The area occurred near the visually evident fire margin occupied by the *P. engelmannii - A. lasiocarpa/Menziesia glabella* h.t., but except for scattered ground surface charcoal, there was little evidence of the fire. The soil was wet throughout the summer, although the standing water decreased through the growing season, and was very calcareous as indicated by 10% HCl application.

6.3.7.3 Snow bed and Avalanche Chute h.t.s

Narrow ravines that contained snow into early summer were common along both sides of the valley slope. The vegetation was variable ranging from shrubs and tree regeneration to grasslands.

In most cases tree seedlings were confined to the slopes and shoulders of the ravines with grass and low shrubs more common along the

ravine base. Both avalanches and summer meltwater are postulated as hindering tree establishment in these areas, and a topographic climax appears likely.

Important species varied with elevation, aspect and avalanche frequency. The more abundant species between about 1340 - 1650 m included *Heracleum lanatum, Ribes lacustre, Rubus strigosus, Mertensia paniculata, Geranium richardsonii, Epilobium angustifolium* and *Elymus innovatus. Juniperus communis, J. horizontalis, Arctostaphylos uva-ursi, Zygadenus elegans, Antennaria lanata* and *Koeleria cristata* typified snow and avalanche chutes on S-facing slopes. Intermediate spruce and *P. engelmannii* seedlings and transgressives occurred on the edges of the ravines, and along with some *A. lasiocarpa* were more abundant on the N exposed slopes. No trees older than 20 years were found and most were aged at about 10 years.

Shrubs were less important above about 1650 m, except on S-exposed slopes. Prominent species of N exposures graded from *Heracleum lanatum, Petasites sagittatus, Delphinium glaucum, Fragaria virginiana* and *Elymus innovatus* at about 1740 m, to *Saxifraga lyallii, Oxyria digyna, Arnica diversifolia, Castilleja occidentalis* and *Equisetum arvense* at about 1900 m elevation. Above 1900 m *Poa alpina, Trisetum spicatum, Luzula wahlenbergii, Silene acaulis, Artimesia norvegica* and *Parnassia fimbriata* were the more important species and graded into the *Dryas hookeriana* dominated alpine tundra.

Snow-bed communities of *Cassiope mertensiana, Phyllodoce empetriformis, P. glandulifera* and *Hylocomium splendens* were common between about 1900 to 2000 m on some of the ridges and slopes above the subalpine meadows and below alpine tundra. The vegetation was most evident on the N exposed slopes of the lateral moraine in the cirques and was mixed with matted *Picea glauca* and *Abies lasiocarpa* on the spur slopes below Gargoyle and Redan Mtns. Other characteristic species included *Myosotis alpestris, Silene acaulis, Salix arctica, Valeriana sitchensis* and *Parnassia fimbriata. Dryas hookeriana* and *D. integrifolia* were more abundant on the steeper slopes and generally increased in cover with elevation, culminating in the formation of the alpine tundra h.t.

Juniperus communis, J. horizontalis and *Arctostaphylos uva-ursi* extended to about 2000 m on S exposures, or nearly to rock and lichen tundra and among scattered patches of *Dryas hookeriana. Salix glauca* and *Shepherdia canadensis* occurred in some of the S exposed avalanche chutes but mostly below about 1800 m. *Zygadenus elegans, Agoseris aurantiaca, Elymus innovatus, Koeleria cristata* and *Trisetum spicatum* also occurred in these areas.

E. SOILS

Soil descriptions were based on stand soil pit data and were classified to the subgroup level where possible. The soils of all stands were not classified due to the inexperience of the author and the absence of reference surveys for the area, but all h.t.s are represented. Parent material included bedrock, colluvium, colluvium-till, till, alluvium and fluvio-lacustrine or lacustrine deposits. Textures were variable ranging from loamy sand to clay with most of the stands containing sandy loam soils (Appendix 4). Neutral or basic conditions were prevalent among the stands on which chemical analyses were completed, with most pH values between 7.0 and 8.6. However, a number of *Picea engelmannii* dominated stands had acidic surface horizons with pH values to 5.2 (Appendix 4). The depth of surface organic horizons was not measured.

1. Regosols

The Regosol Order was fairly widespread, occurring throughout the elevational range of sampled areas and on colluvium-till, colluvium, alluvium, lacustrine and bedrock parent materials (Table 13). Four subgroups were identified within the drainage basin and are described below.

Orthic Regosols occurred on glaciofluvial terraces (stand 6), on stable colluvial slopes (stand 15) and steep colluvial slopes (stands 29 and 31). The soils were characterized by having a uniform color and no distinct horizon development and/or by containing pebbles and rocks

Table 13. Soil Orders and Subgroups, and associated landforms of the h.t.s.

Soil Type	Landform	Habitat Type
Regosols		
Orthic Regosol	Glacio-fluvial Terraces	*Au-u - Cp*
	Constant Colluvial Blanquet	*Pm/Ei, P - Pa/Jo/Ei, Pe - Al/Ad/He*
Cumulic Regosol	Alluvial Terrace	*Pg/Cw / Lb*
	Glacio-fluvial Terrace	*Au-u - Cp*
	Colluvial Veneer over Bedrock	*(Dryas hookeriana - Oxytropis podocarpa)*
Lithic Regosol	Colluvial Veneer over Bedrock	*Pm/Ei, P - Pa/Jo/Ei*
Cryic Regosol	Lacustrine Plain	*Sg/Ei*
Luvisols		
Gray Luvisol	Constant Colluvial Blanquet	*Pg/Lb/He, Pg/Lb - Ei, Pm/Ei*
	Colluvial Blanquet & Fan	*Pm/Ei*
Brunisols		
Orthic Eutric Brunisol	Glacio-fluvial Terrace	*Pg/Lb/He*
	Alluvial Plain	*Pm/Jo/Cp*
	Constant Colluvial Blanquet	*Pe - Al/Mg - Vm, Pe - Al/Ao*
Degraded Eutric Brunisol	Colluvial Blanquet & Fan	*Pm/Jo/Cp, Pm/Ei, Pg/Ei/Co*
	Colluvial Blanquet	*Pe - Al/Mg - Vm, Pe - Al/Ao, Pe - Al/Ad/He*
Alpine Eutric Brunisols	Lacustrine Plain	*Sv/Pa*

throughout the profile. The Subgroup encompasses a number of associations, occurring in *Arctostaphyloe uva-ursi - Calamagrostis purpurascens, Pseudotsuga menziesii/Elymus innovatus, Picea - Pinus albicaulis/Juniperus communis/Elymus innovatus, Picea engelmannii - Abies lasiocarpa/Menziesia glabella - Vaccinium membranaceum* and *Picea - Abies/Arnica diversifolia/Hylocomium splendens* h.t.s (Table 13). An example of the profile from stand 6 is described below:

Horizon	Thickness (cm)	Description
L-H	3	Grayish brown (10 YR 5/2, dry), fibrous roots, pH 8.4.
CX	at 3	Light grayish brown (10 YR 6/2, dry), sandy loam, rocky glacial till, pH 8.6.

Cumulic Regosols were found in three stands and result from the burying of a developing Ah horizon by mineral deposition. Stand 1, containing a mature *Picea glauca* forest, is subjected to aeolian loess deposits from Jasper Lake during winter and early spring when water levels are low. Soil profiles of stand 3, on a steep slope of a glaciofluvial terrace containing till, and an alpine community on a rock shattered slope exhibited evidence of down slope soil movement. Thus the Ah horizons have been buried by colluvium in stand 3 and by frost associated solifluction at the alpine site.

The Cumulic Regosol Subgroup occurred in *Picea glauca/Linnaea borealis/Hylocomium splendens, Arctostaphyloe uva-ursi - Calamagrostis purpurascens* h.t.s, and in a *Dryas hookeriana - Oxytropis podocarpa* stand which represented an alpine area (Table 13). The profiles of the two h.t.s were different, being mostly of coarse soil in stand 1 and

rock in stand 3 and the alpine site. Some staining below the Ah horizons had occurred in some of the profiles, indicating a possible trend toward a Bm horizon and the Brunisolic Order. The soil is represented by the alpine *Dryas - Oxytropis* stand profile below:

Horizon	Thickness (cm)	Description
L-H	6	Fibrous root and leaf litter, ...
Ah	6	Dark brown (10 YR 3/3, dry), loam, pH 6.6.
Ck	8	Gray (10 YR 6/1, dry) sandy loam, pH 7.2.
Ahb	2	Yellowish brown (10 YR 5/4, dry), loam, pH 7.5.
Ck	at 22	Gray (10 YR 6/1, dry) sandy loam with angular rock.

A Lithic Regosol was indicated for stands 18 and 32 which were designated as *Picea glauca/Elymus innovatus/Cornus canadensis* and *Picea - Pinus albicaulis/Juniperus communis/Elymus innovatus* h.t.s respectively. Both areas contained thin colluvial veneer over bedrock with the soil of stand 32 illustrating the profile type below:

Horizon	Thickness (cm)	Description
L-H	2	Dark grayish brown (10 YR 4/2, dry), fibrous roots and needle litter, loam.
(Ae)	2	Very pale brown (10 YR 8/3, dry), loam, slightly hard granular, pH 7.3.
Ck	at 4	Dark brown (10 YR 3/3, dry), loam, numerous rocks, pH 6.0.

Soil of the *Salix glauca/Elymus innovatus* h.t. was placed within the Cryic Regosol Subgroup due to the presence of permafrost. No horizon differentiation was recognized except for an Ah near the surface. The profile of stand 26 is described as follows:

Horizon	Thickness (cm)	Description
L-H	3	Dark grayish brown (10 YR 4/2 dry), deciduous leaf litter and fibrous roots ....
Ah	4	Very dark grayish brown (10 YR 3/2, dry), silty loam, pH 7.6.
Ck	19	Dark grayish brown (10 YR 4/2, dry), silty loam, pH 7.1.
Cz	at 26	Very dark grayish brown (10 YR 3/2, dry), frozen ....

2. Luvisols.

The Luvisol Order was not well represented with only Gray Luvisol soils recognized within the drainage basin. The soil was confined to forests of the lower elevations (1200 to 1430 m) on SE to NE-facing slopes. Stands 7, 10; 9, 11; 16 of the *Picea glauca/Linnaea borealis/Hylocomium splendens*, *Picea glauca/Linnaea borealis - Elymus innovatus* and *Pseudotsuga menziesii/Elymus innovatus* h.t.s respectively were represented (Table 13). Most of the stands occurred on the lower portion of the constant colluvial slopes or on the adjacent concave waxing slope and had colluvial parent material mixed with till. The profile described below is that of stand 11.

Horizon	Thickness (cm)	Description
L-F	2	Conifer needle litter, some charcoal .....
Ae	14	Yellowish brown (10 YR 5/6, dry), sandy clay loam, friable, pH 8.2
Bt	24	Brownish yellow (10 YR 6/8, dry), sandy clay loam, slightly hard platy, pH 8.6.
Ck	at 40	Very pale brown (10 YR 7/4, dry), sandy loam, calcareous ....

3. Brunisols

Brunisols were nearly as extensive as Regosols and were especially prevalent in the *Picea* and *Picea engelmannii - Abies lasiocarpa* Series (Table 13). Orthic Eutric Brunisol, Degraded Eutric Brunisol and Alpine Dystric Brunisol Subgroups were recognized from the soil profiles. Some classification problems resulted due to transition between Brunisolic and Luvisolic profile conditions, especially on the more recently burned areas which have probably been affected more by sheet erosion and leaching of the A horizon. However, the low percent of clay in the B horizon was used to diagnose a Brunisolic affinity in the burned stands.

An Orthic Eutric Brunisol occurred within *Picea glauca/Linnaea borealis/Hylocomium splendens* (stand 5), *Pseudotsuga menziesii/Juniperus communis/Calamagrostis purpurascens* (stand 2), *Picea engelmannii - Abies lasiocarpa/Menziesia glabella - Vaccinium membranaceum* (stand 23, 24), and *Picea - Abies/Arnica cordifolia* (stand 30) h.t.s. The stands occurred within the glaciofluvial terrace (5), alluvial plain (2) and constant colluvial blanquet landform units (23, 24 and 30). Parent

material therefore included fluvial-lacustrine, alluvium deposits and colluvium over bedrock. Stand 2 is described below as the subgroup profile type:

Horizon	Thickness (cm)	Description
L-H	1	Conifer needle litter .....
Ah	6	Brown (10 YR 5/3, dry), weak platy, sandy loam, pH 7.7.
Bm	24	Brownish yellow (10 YR 6/8, dry), friable, sandy loam, pH 8.0.
Ck	at 30	Light gray (10 YR 7/2, dry), rocky, sandy loam, pH 7.9.

Degraded Eutric Brunisols were distinguished primarily on the basis of containing an Ae horizon over a Bm. A large number of stands were defined as containing this Soil Subgroup (4, 8, 12, 13, 14, 21, 22, 25 27, 33) and thus portions of the *Pseudotsuga menziesii*, *Picea glauca*, and *Picea engelmannii - Abies lasiocarpa* Series were represented (Table 13). The sites were predominantly on the lower portion of the constant colluvial slope and on the lower adjacent concave waxing slope and contained colluvium and sheet wash deposits over till as parent material. The L-F horizon contained pieces of charcoal in the more recently burned areas (*Picea - Abies/Menziesia - Vaccinium*; 21 and 22) and the A horizon in general was pale brown indicating some eluviation. However, the relatively low amount of clay in the B horizon as well as the yellow chroma precluded a Luvisolic soil and a Degraded Eutric Brunisol was designated. The profile of stand 8 describes the Soil Subgroup.

Horizon	Thickness (cm)	Description
L-H	3	Conifer needle litter, moss .....
Ae	7	Light yellowish brown (10 YR 6/4, dry), weak fine granular sandy loam, pH 7.6.
Bm	22	Strong brown (7.5 YR 5/6, dry), friable, sandy loam, pH 9.0.
Ck	at 32	Grayish brown (10 YR 5/2, dry), rocky, sandy loam, very calcareous .....

Alpine Eutric Brunisols were identified for the subalpine meadows containing the *Salix vestita/Poa alpina* h.t. (stand 34 and 35; Table 13). A thick Ah horizon over a Bm characterized the soil profile. Both sites occurred within glacial cirques on lacustrine over bedrock parent material. Data from stand 34 were used to describe the soil profile below:

Horizon	Thickness (cm)	Description
L-H	2	Fibrous roots - litter .....
Ah	14	Dark brown (10 YR 4/3, dry), soft crumbly, silt loam, pH 5.6.
Bm	24	Brownish yellow (10 YR 6/6, dry), friable, loam, pH 6.3.
Ck	at 40	Light yellowish brown (10 YR 6/4, dry), structureless, some rocks, sandy clay loam, pH 7.8.

F. INTEGRATION OF RESULTS

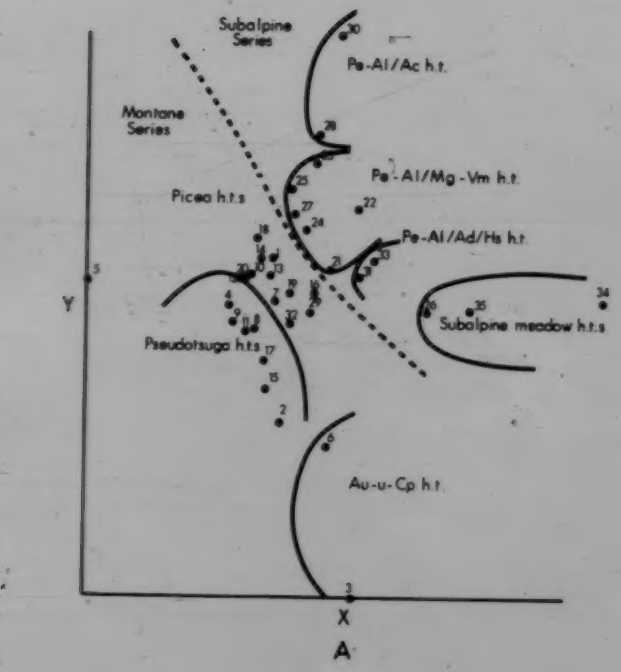
The relationships between and among environmental and vegetational variables were assessed by plotting factors on the stand ordination field and using simple correlation. Both techniques identify potentially causal relationships, but it is realized that other unknown factors may also be operative on the variables being investigated (Beil 1966).

1. Community Distribution

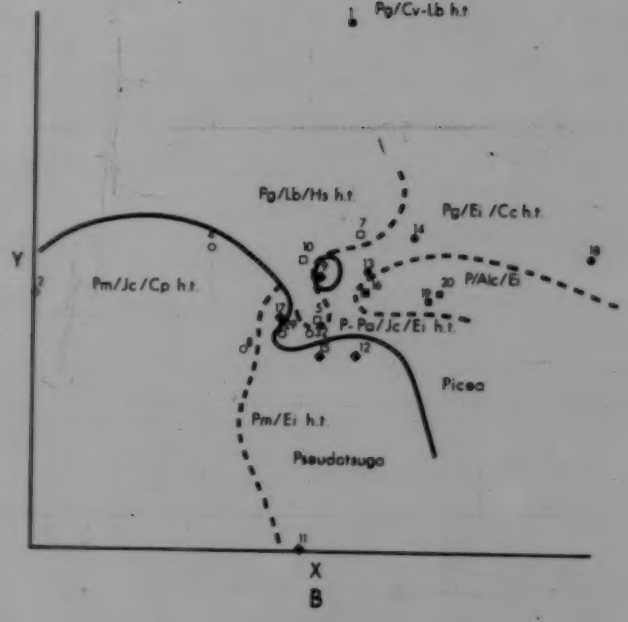
The stand ordination was used to investigate the relationships of stands and their habitat types (h.t.s). Subalpine and montane Series are clearly separated on the field (Fig. 14). Furthermore, stands comprising the three subalpine forest and two meadow h.t.s are well delimited within the subalpine matrix. Although the three Series comprising the montane vegetation are well delimited, the respective h.t.s are not. Inspection of the stand placement on the field indicates a hot-xeric, to mesic, to cool-hydric h.t. gradient from lower center to upper left to right center respectively (Fig. 14).

Stands on the lower left portion of the field occurred mostly at the lower elevation of the basin and usually had S-aspects. The latter was especially true of those stands in the lower portion of the *Pseudotsuga* series (i.e. 3, 15, 17). Stands to the right center of the field were either at the higher elevation of the basin or were in drainage basins which received both meltwater and cold air from adjacent slopes.

Figure 14. Separation of all stands into series and h.t.s on the ordination field. Stand 5 and 34 were designated as end stands of the x axis (A), and the h.t. pattern displayed by ordinating only stands of the *Picea* and *Pseudotsuga* (montane) Series (B).


Subalpine Series
Montane Series
Picea h.t.s
Pseudotsuga h.t.s
Pe-Al/Ac h.t.
Pe-Al/Mg-Vm h.t.
Pe-Al/Ad/Hs h.t.
Subalpine meadow h.t.s
Au-u-Cp h.t.
Y
X

A


Pg/Cv-Lb h.t
Pg/Lb/Hs h.t.
Pg/Ei /Cc h.t.
Pm/Jc/Cp h.t.
P/Alc/Ei
P-Pg/Jc/Ei h.t.
Picea
Pm/Ei h.t.
Pseudotsuga
Y
X

B

The stands of the montane Series were ordinated separately to try and better ascertain h.t. affinities (Fig. 14B). As with the total stand ordination, the intermediacy of a number of these stands remains obvious. Stand 5 is intermediate to the *Pseudotsuga* and *Picea glauca* series due to a recent fire history and its xerophytic nature. *Juniperus communis, Rosa acicularis, Shepherdia canadensis* and especially a relatively high cover of *Elymus innovatus* caused this intermediacy. This stand was placed in the *Pg/Lb/Hs* h.t. on the basis of *P. glauca* regeneration and similarity to the other stands of the h.t. on a total floristic basis (see Table 11, p. 105).

In other cases, however, the stands were grouped into their respective h.t.s on the ordination field (Fig. 14B). The xeric nature of the *P-Pa/Jc/Ei* h.t. was illustrated on the ordination as a close relationship to the elevationally lower *Pm/Ei* h.t. Both were found on the more xeric S exposed slopes in relation to the geographically adjacent *Picea - Abies* and *Picea* h.t.s.

Both ordinations exhibited a tendency for the stands to be centrally clustered. This is probably an artifact of the method as discussed by Gauch and Whittaker (1972) and becomes more acute with increased *beta* diversity (i.e. the range of community types in the analysis).

A number of plant stratum and attributes of important species showed clearcut patterns in the ordination. Except for the more ubiquitous species, most were also associated with h.t. nomenclature, reinforcing the classification.

1.1 Tree Stratum

No distinct pattern was exhibited on the ordination by total tree cover (Fig. 15). Basal area values were generally highest to the left center of the ordination; in the montane forest Series. The stand age pattern was the opposite; the older trees occurring predominantly in the upper portion of the field in subalpine forest stands (Fig. 15).

The *Picea-Abies* h.t.s exhibited the most even cover classes except in the more open subclimax areas. Canopy cover of the *Pseudotsuga* series was the most variable having some very open stands. The relationship between tree cover and ESA was positive, but not strongly so ($r = +.35$); both relatively young and old stands exhibited high cover values.

The largest basal area values were within the montane forest Series, but no consistent pattern was associated with series or h.t. placement on the ordination field (Fig. 15). Both the younger and older stands exhibited high basal areas values and thus correlation between total basal area and ESA was insignificant ($r = +.01$). However, positive relationships were often indicated for mean age and basal area for a number of species, but these correlations were not often significant (Table 14). Apparently the dense character of the younger stands containing *Pinus contorta* is a significant factor in the relationship. *Picea glauca* and *P. menziesii* basal areas were very positively correlated ($r = +.90$, $p > 0.01$), indicating their close association in the montane forest.

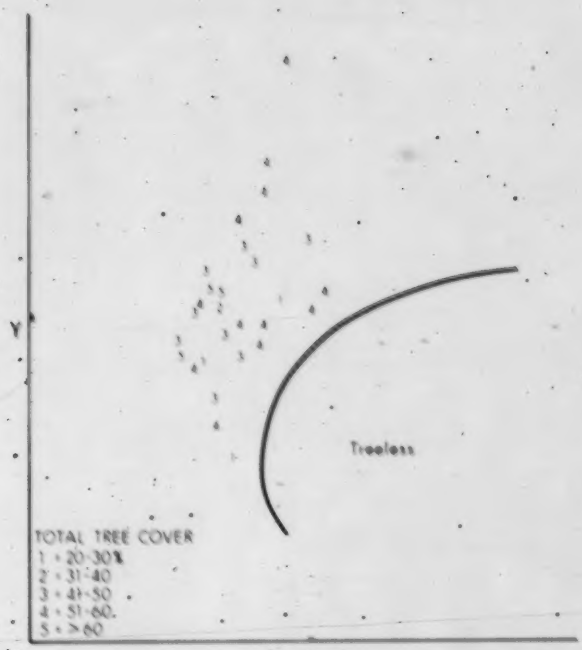
Table 14. Simple correlation between selected vegetation attributes and several physical characteris
indicated by * at the 5% level and ** at the 1% level. The number of observations ran
comparisons where less than 3-observations were involved have no values. Missing values due to the
the area sampled cause the reduction on number in observations.

		1	2	3	4	5	6	7	8	9	10	11
Elevation (m)	1	.	.	.	.	.	.	.	.	.	.	.
Slope	2	+.36*	.	.	.	.	.	.	.	.	.	.
Degrees from south	3	+.28	+.08	.	.	.	.	.	.	.	.	.
% Sand (top mineral horizon)	4	-.45**	-.12	+.02	.	.	.	.	.	.	.	.
% Clay (top mineal horizon)	5	+.15	+.02	-.15	-.71**	.	.	.	.	.	.	.
% Tree - tall shrub cover	6	-.21	+.23	+.01	-.01	-.11	.	.	.	.	.	.
Picea glauca basal area	7	-.57	-.35	-.40	+.57	-.19	+.02	.	.	.	.	.
P. glauca x engelmannii basal area	8	+.48	+.41	+.02	+.02	-.53	+.20	-	.	.	.	.
Pinus contorta basal area	9	-.35	-.17	+.07	-.20	+.01	+.24	-.63*	-.11	.	.	.
Pseudotsuga menziesii basal area	10	-.42	-.32	+.16	+.49	-.32	+.17	+.90**	-	-.36	.	.
Picea engelmannii basal area	11	-.55	-.71	-.57	-.30	+.45	-.51	-	-	-	-	.
Abies lasiocarpa basal area	12	+.15	-.41	+.23	-.32	+.19	+.22	-	-.04	-.59	-	+.31
Picea glauca $\bar{x}$ age	13	-.65	-.44	-.62	+.59	-.55	+.07	+.96**	-	-.63	+.90	.
P. glauca x engelmannii $\bar{x}$ age	14	+.17	-.10	-.47	-.15	-.32	+.62	-	+.38	+.46	-	.
Pinus contorta $\bar{x}$ age	15	-.34	-.05	-.05	+.38	-.19	+.16	+.92**	+.57	-.35	+.82**	.
Pseudotsuga menziesii $\bar{x}$ age	16	-.43	-.12	+.51	+.75	-.33	+.01	+.96**	-	-.89**	+.96**	.
Picea engelmannii $\bar{x}$ age	17	-.35	-.66	+.18	+.09	-.24	+.39	-	-	-	-	+.41
Abies lasiocarpa $\bar{x}$ age	18	-.44	-.06	+.11	-.11	-.16	+.02	-	-	-	-	+.25
Linnaea borealis $\bar{x}$ cover	19	-.56**	-.32	-.05	+.17	+.09	+.22	+.05	-.34	+.56**	+.13	+.83
Arctostaphylos uva-ursi $\bar{x}$ cover	20	-.40	+.03	-.66	-.11	+.35	-.82**	+.02	-	-.36	-.47	.
Elymus innovatus $\bar{x}$ cover	21	-.08	+.17	-.15	-.06	+.21	+.14	-.38	-.32	+.39	-.40	+.03
Calamagrostis purpurascens $\bar{x}$ cover	22	+.45	-.78	+.57	+.56	-.54	+.42	-	-	+.94*	-.96*	.
Arnica cordifolia $\bar{x}$ cover	23	+.15	+.23	-.14	-.44*	+.25	+.18	+.16	+.50	+.05	+.10	+.83
Juniperus communis $\bar{x}$ cover	24	-.07	-.06	-.05	-.01	+.17	-.31	-.21	+.57	-.33	-.35	.
Menziesia glabulla $\bar{x}$ cover	25	-.11	+.13	+.40	+.10	-.07	-.39	-	+.62	-.38	-	-.07
Vaccinium membranaceum $\bar{x}$ cover	26	-.17	-.23	-.11	+.15	-.14	-.08	-	+.97**	-.02	-	+.51
Hylocomium splendens $\bar{x}$ cover	27	-.10	-.26	+.05	-.14	+.03	+.25	-.04	-.06	+.31	+.62*	+.47
Shepherdia canadensis $\bar{x}$ cover	28	-.07	-.14	+.16	-.18	+.10	+.22	-.13	-.18	+.40	-.43	.
Alnus spp. $\bar{x}$ cover	29	+.25	+.31	+.15	+.02	+.44	-.57	-.70	-	+.41	-.82	.
Cornus canadensis $\bar{x}$ cover	30	+.02	-.27	+.08	+.24	+.09	-.64**	+.21	+.16	+.07	+.37	+.85

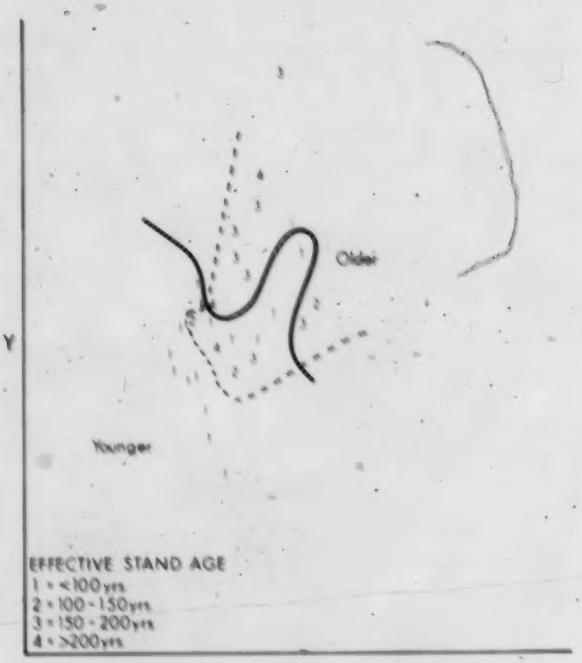
haracteristics. Significance is
s ranged from 2 to 36 and thus
ue to the elevational range of

10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
-	+.31																		
.90																			
-	-	+.93	-																
.82**	-	+.99*	+.86*	+.27															
.96**	-	-	+.99*	-	+.89**														
-	+.41	+.81*	-	-	-	-													
-	+.25	+.13	-	-	-	-	+.69												
.13	+.83	+.03	+.24	-.26	+.14	+.19	+.12	-.26											
.47	-	-	+.12	-	-.25	-.75	-	-	-.65										
.40	+.03	-.62	-.15	-.28	-.31	-.33	-.65	+.27	+.55**	-.48									
.96*	-	-	-	-	-.90*	-.96*	-	-	+.37	-.95*	+.55								
.10	+.83	+.52	-.78	+.28	-.19	+.99**	+.59	+.18	-.07	-.36	+.04	-							
.35	-	-.36	-.34	-.20	-.13	-.19	-	-	+.18	-.13	+.01	+.74	+.15						
-	-.07	-.40	-	+.15	+.67	-	+.58	+.91**	-.40	-	-.21	-	-.31	-.99*					
-	+.51	+.15	-	+.48	+.40	-	+.63	+.61	+.09	-	-.18	-	+.16	-.70	+.32				
.62*	+.47	+.48	-.35	+.81	-.06	+.70*	+.65	+.34	-.15	-.63	-.14	-.96*	+.11	-.30	-.05	+.21			
.43	-	-.09	-.46	-.16	-.21	-.35	-	-	-.11	-.02	-.01	+.57	+.13	-.22	-.07	+.22	+.97**		
.82	-	-	-.70	-	-.57	-.98*	-	-	+.36	-.48	+.47	-	-.30	+.76	-	-	.22	-.06	
+.37	+.85	-.19	+.33	-.43	-.11	+.83	+.34	-.55	+.05	-.36	+.34	-	-.08	-.44	-.03	+.14	+.09	+.15	+.01

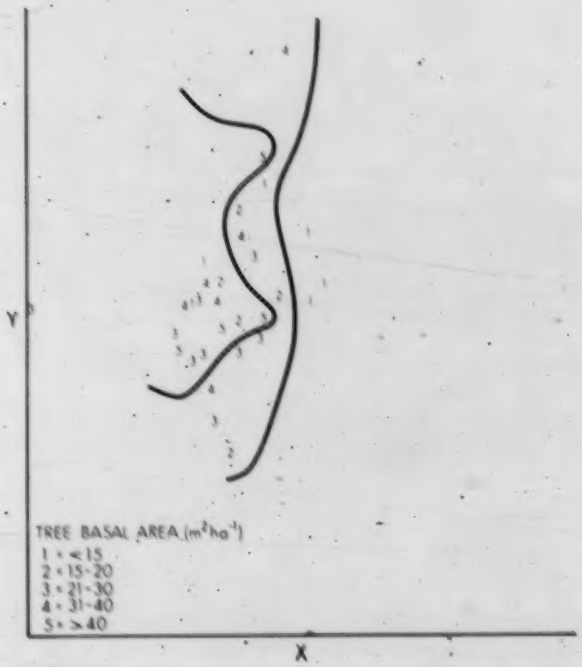
Figure 15. Ordination pattern of total tree cover classes (A), ESA (effective stand age) class (B) and tree basal area classes (C).


Y
Treeless
TOTAL TREE COVER
1 = 20-30%
2 = 31-40
3 = 41-50
4 = 51-60
5 = >60
X

A.


Y
Older
Younger
EFFECTIVE STAND AGE
1 = <100 yrs
2 = 100 - 150 yrs
3 = 150 - 200 yrs
4 = >200 yrs
X

B


Y
TREE BASAL AREA ($m^2 ha^{-1}$)
1 = <15
2 = 15-20
3 = 21-30
4 = 31-40
5 = >40
X

C

Pinus contorta cover values were higher in the montane *Picea* and *Pseudotsuga* Series and greatest in the *Fg/Fi/Cc* h.t. (Fig. 16). The highest cover values were often shown by young stands (Fig. 15), and *P. contorta* was strongly negatively correlated with ESA' ($r = -.59$, $p > 0.01$), as might be expected in a successional species.

Picea engelmannii and *Abies lasiocarpa* usually occurred together, but their cover values were not significantly correlated ($r = +.25$, $p > 0.05$). In some stands, low cover values in one species was compensated for by high cover in the other (Fig. 16), such that total cover did not vary greatly in the *Picea-Abies* Series, as noted above.

1.2 Shrub Stratum

Cover values of several dominant shrub species exhibited either a montane or subalpine Series affiliation on the ordination field. Species more common in the *Pseudotsuga* and *Picea* Series, or lower left on the ordination field included *Rosa acicularis*, *Shepherdia canadensis* and *Juniperus communis* (Fig. 17). Of these, *Rosa acicularis* was the most restricted, occurring in only one stand of the *Picea-Abies* h.t.s (Fig. 17). Conversely, *Vaccinium membranaceum*, *Menziesia glabella* and *Rhododendron albiflorum* occurred primarily in the upper right, or *Picea-Abies* portion of the ordination field (Fig. 18).

Vaccinium membranaceum cover was significantly correlated with *P. glauca* x *engelmannii* age ($r = +.91$, $p < 0.01$) and basal area ($r = +.92$, $p < 0.01$). The occurrence of both *V. membranaceum* and *Menziesia glabella*

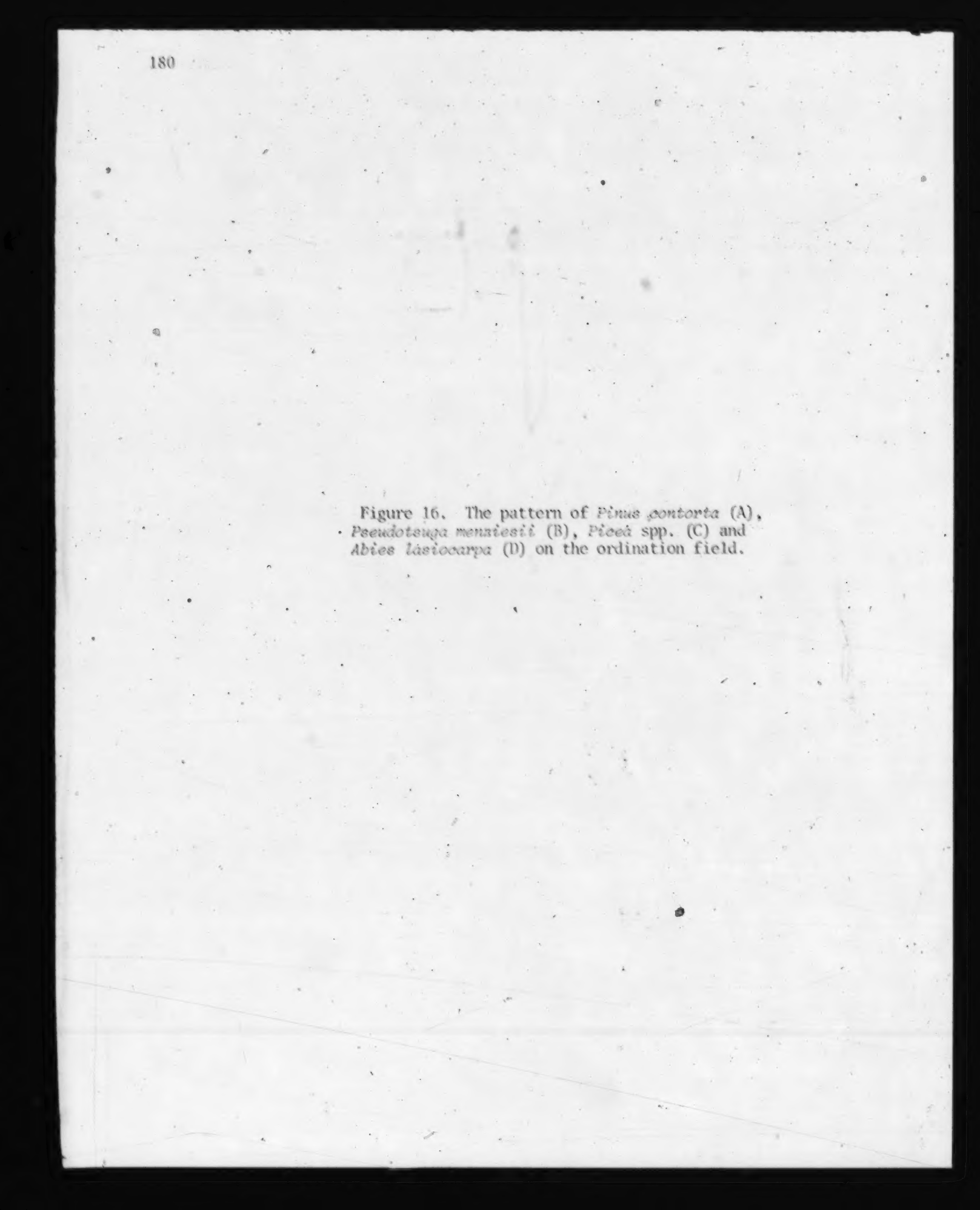
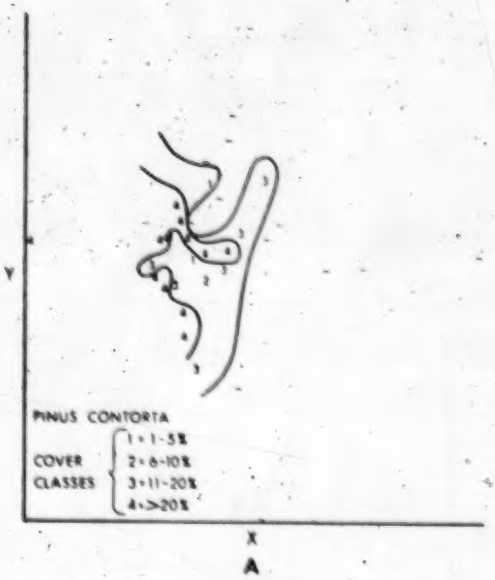
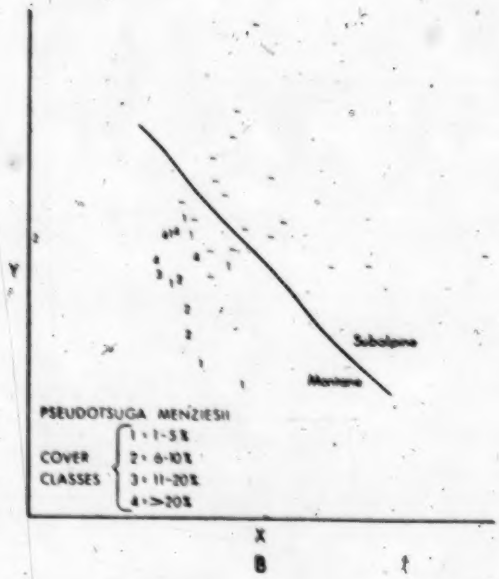


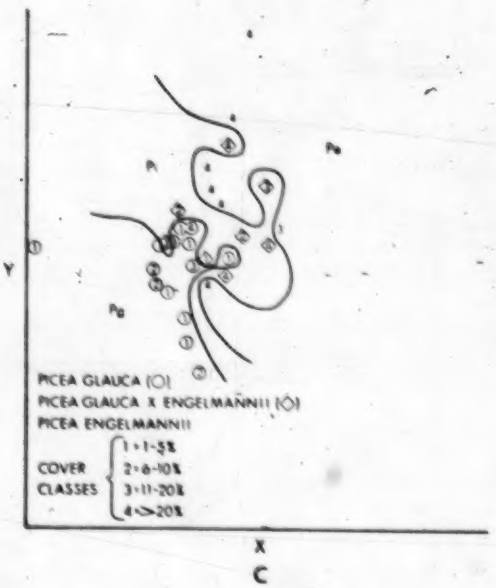
Figure 16. The pattern of *Pinus contorta* (A), *Pseudotsuga menziesii* (B), *Picea* spp. (C) and *Abies lasiocarpa* (D) on the ordination field.


Y
X
PINUS CONTORTA
COVER CLASSES
1 = 1-5%
2 = 6-10%
3 = 11-20%
4 = >20%

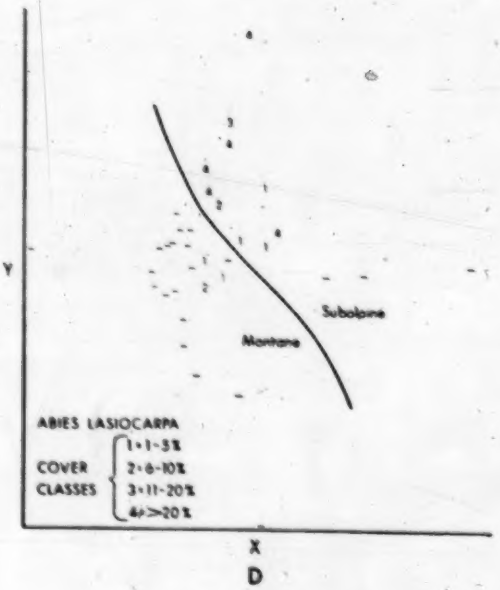
A


Y
X
Subalpine
Montane
PSEUDOTSUGA MENZIESII
COVER CLASSES
1 = 1-5%
2 = 6-10%
3 = 11-20%
4 = >20%

B

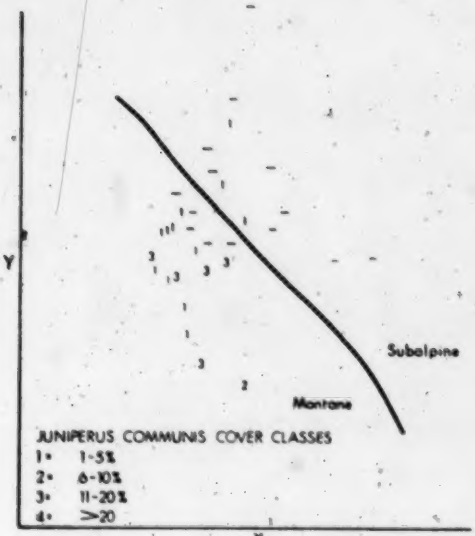

Y
X
PICEA GLAUCA (O)
PICEA GLAUCA X ENGELMANNII (Ó)
PICEA ENGELMANNII
COVER CLASSES
1 = 1-5%
2 = 6-10%
3 = 11-20%
4 = >20%

C

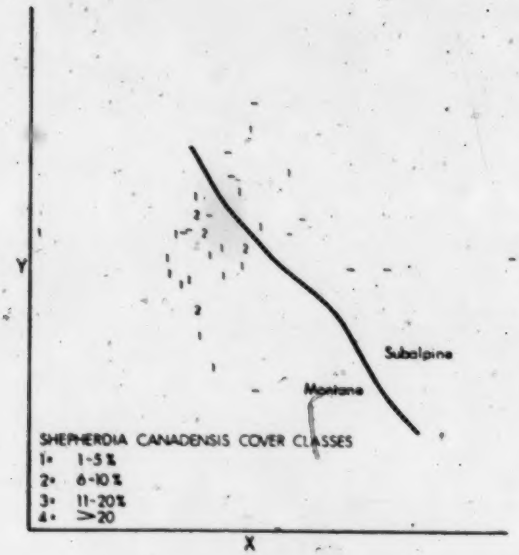

Y
X
Subalpine
Montane
ABIES LASIOCARPA
COVER CLASSES
1 = 1-5%
2 = 6-10%
3 = 11-20%
4 = >20%

D

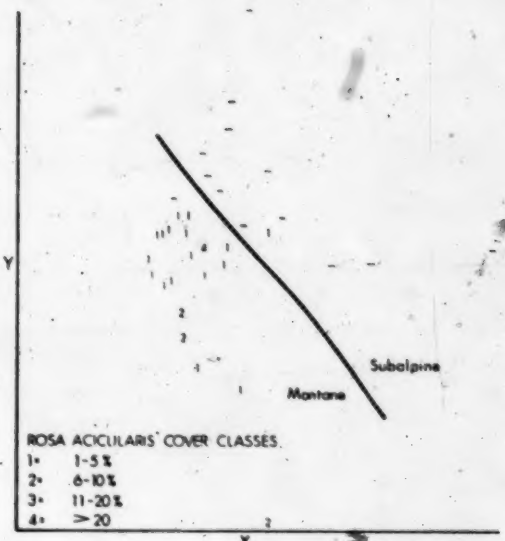
Figure 17. Cover class pattern of *Juniperus communis* (A), *Shepherdia canadensis* (B), *Rosa acicularis* (C) and *Alnus crispa* (D) on the ordination field.


Y
Subalpine
Montane
JUNIPERUS COMMUNIS COVER CLASSES
1• 1-5%
2• 6-10%
3• 11-20%
4• >20
X

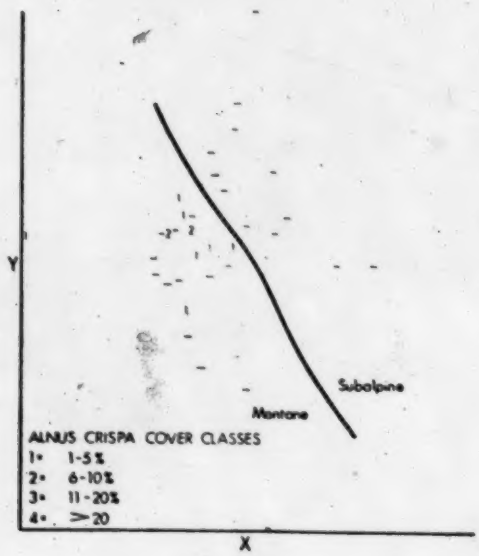
A


Y
Subalpine
Montane
SHEPHERDIA CANADENSIS COVER CLASSES
1• 1-5%
2• 6-10%
3• 11-20%
4• >20
X

B

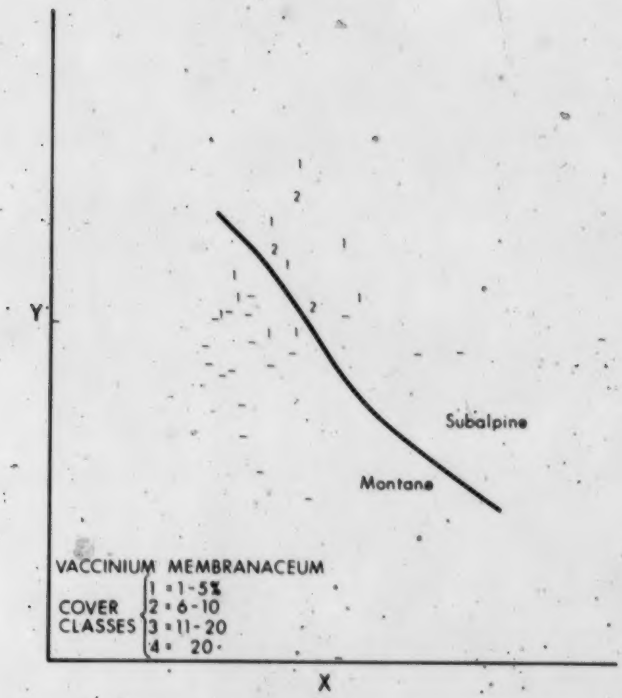

Y
Subalpine
Montane
ROSA ACICULARIS COVER CLASSES
1• 1-5%
2• 6-10%
3• 11-20%
4• >20
X

C

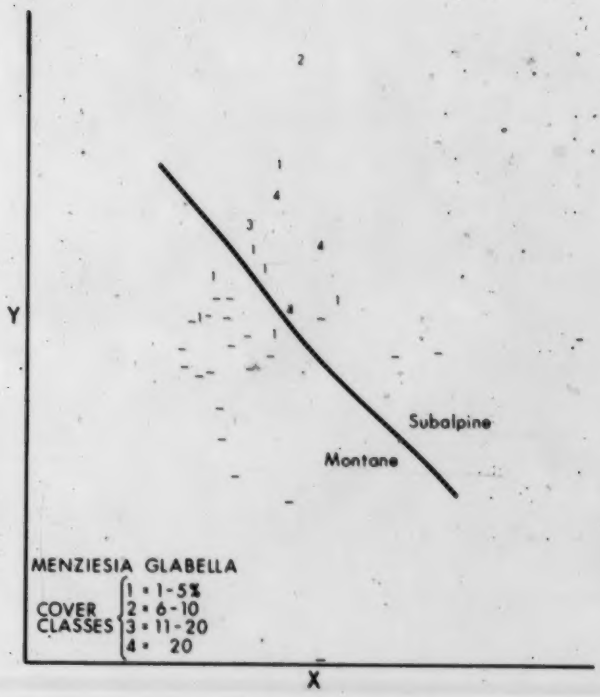

Y
Subalpine
Montane
ALNUS CRISPA COVER CLASSES
1• 1-5%
2• 6-10%
3• 11-20%
4• >20
X

D

Figure 18. Cover class pattern of *Vaccinium membranaceum* (A) and *Menziesia glabella* (B) on the ordination field.


Y
Subalpine
Montane
VACCINIUM MEMBRANACEUM
COVER CLASSES
1 = 1-5%
2 = 6-10
3 = 11-20
4 = 20
X

A


Y
Subalpine
Montane
MENZIESIA GLABELLA
COVER CLASSES
1 = 1-5%
2 = 6-10
3 = 11-20
4 = 20
X

B

as an integral part of some *Picea-Abies* h.t.s was thus corroborated by simple correlation analysis of species attributes (Table 14). Montane shrubs were not as well related to individual tree species' attributes, being more widely distributed among the *Pseudotsuga* and *Picea* h.t.s (Table 15).

Juniperus communis, and to a lesser extent *Rosa acicularis*, had higher cover values in younger stands at the lower left on the ordination (see Fig. 15). However, this relationship was probably more ecologic than historic, and there was no significant correlation between tree ages and these shrub species' cover values (Table 14).

1.3 Herb-Low Shrub and Bryoid Strata

As with the dominant shrubs, a number of ground cover species were closely affiliated with either montane or Subalpine Series. *Arctostaphylos uva-ursi*, *Calamagrostis purpurascens* and *Aster conspicuus* had a montane pattern on the ordination field (Fig. 19). *Linnaea borealis* and *Elymus innovatus* exhibited a wider distribution, but had higher cover values in stands of the montane Series (Figs. 19 & 20). The converse of this was shown by *Arnica cordifolia* and *Cornus canadensis* cover, with a tendency to affiliate with the *Picea-Abies* series (Fig. 20). *Hylocomium splendens* was quite ubiquitous (Fig. 20), but had higher cover values in older stands, especially those of the *P. menziesii* h.t.s (Table 14). Significant, positive relationships were indicated between cover values of *Linnaea borealis* and *Elymus innovatus* ($r = +.55$, $p < .01$). Cover values of *Arctostaphylos uva-ursi* and *Calamagrostis purpurascens* were

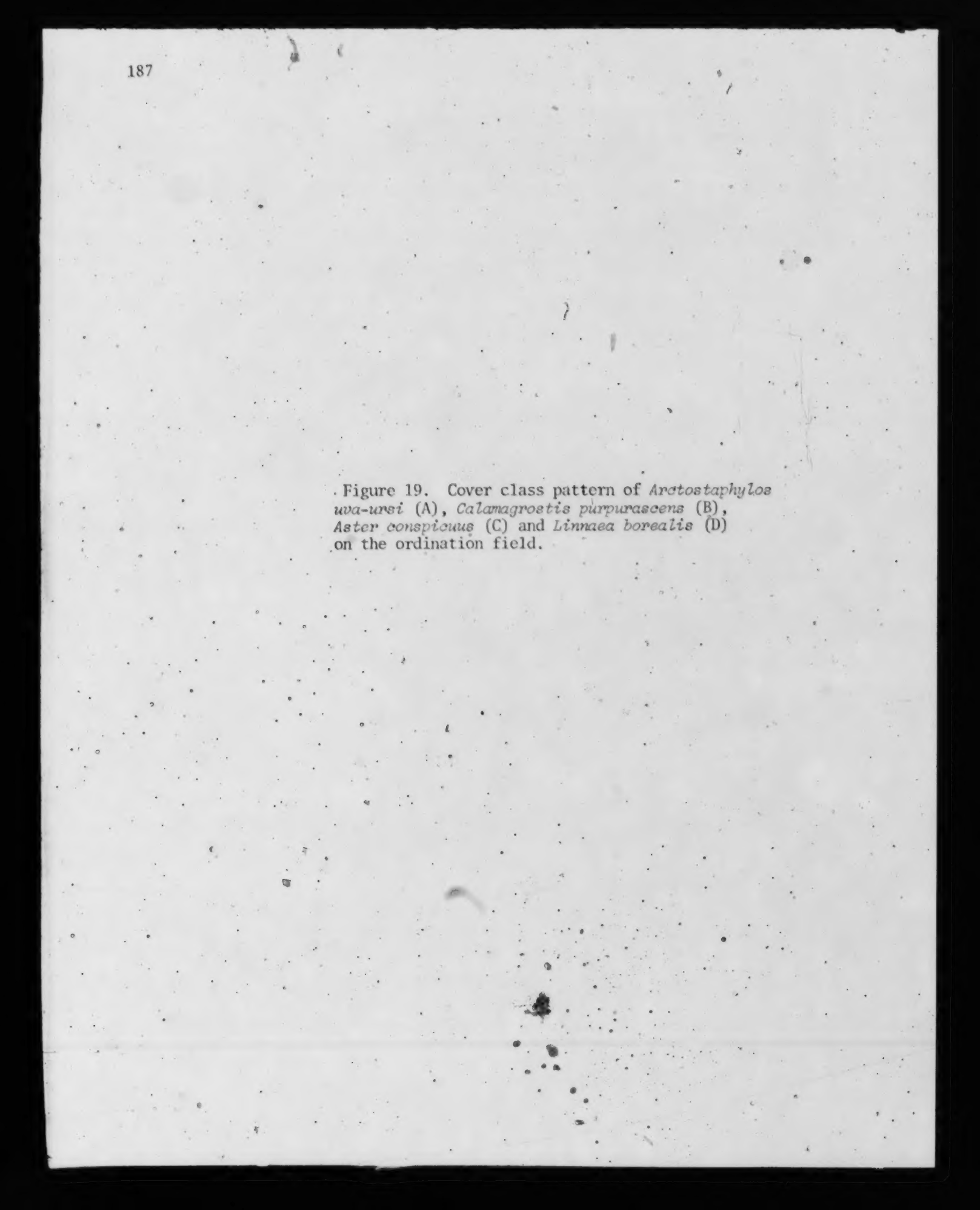
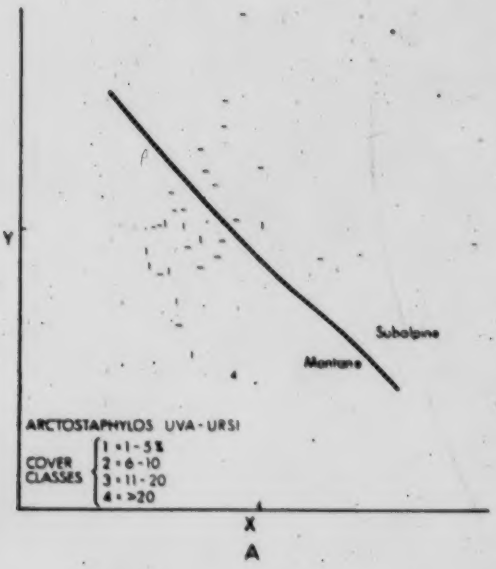
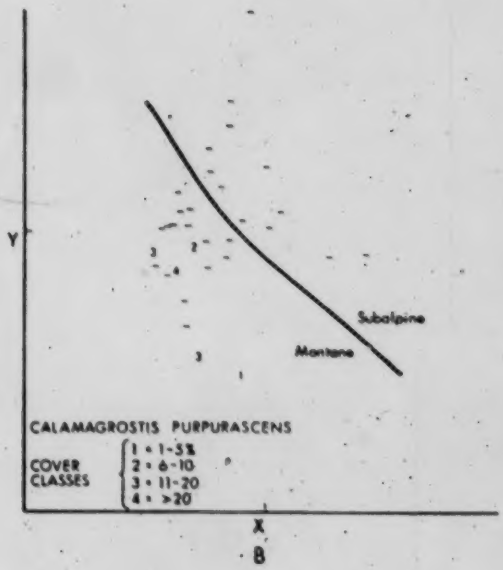
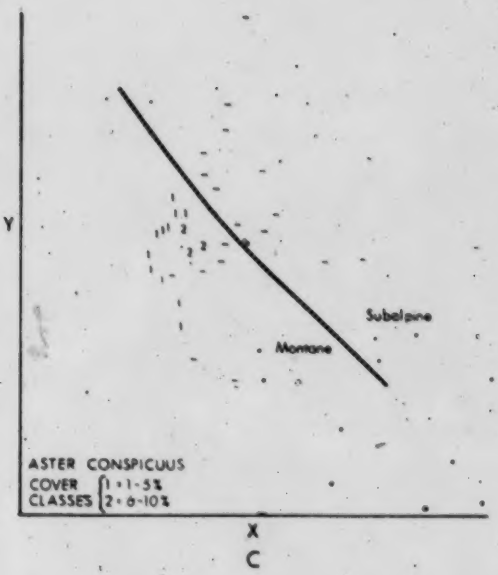


Figure 19. Cover class pattern of *Arctostaphylos uva-ursi* (A), *Calamagrostis purpurascens* (B), *Aster conspicuus* (C) and *Linnaea borealis* (D) on the ordination field.


Y
Subalpine
Montane
ARCTOSTAPHYLOS UVA-URSI
COVER CLASSES
1 = 1-5%
2 = 6-10
3 = 11-20
4 = >20
X
A


Y
Subalpine
Montane
CALAMAGROSTIS PURPURASCENS
COVER CLASSES
1 = 1-5%
2 = 6-10
3 = 11-20
4 = >20
X
B


Y
Subalpine
Montane
ASTER CONSPICUUS
COVER CLASSES
1 = 1-5%
2 = 6-10%
X
C

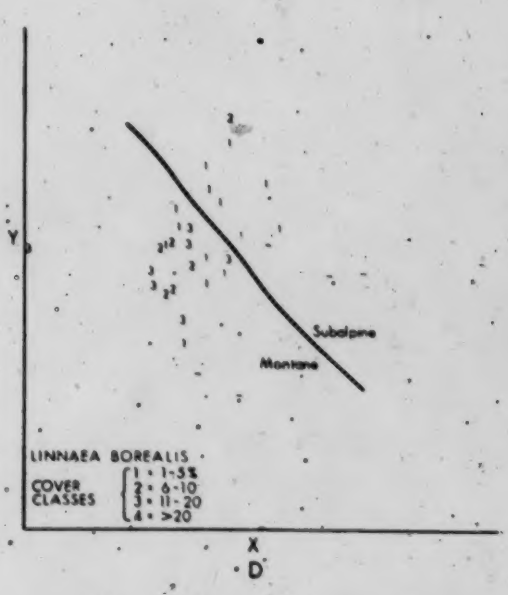
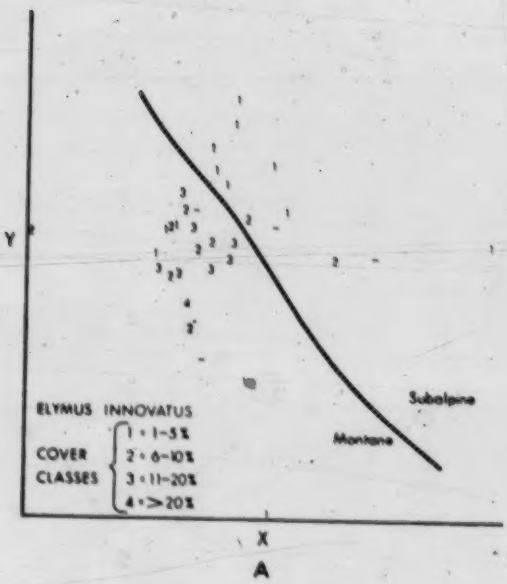
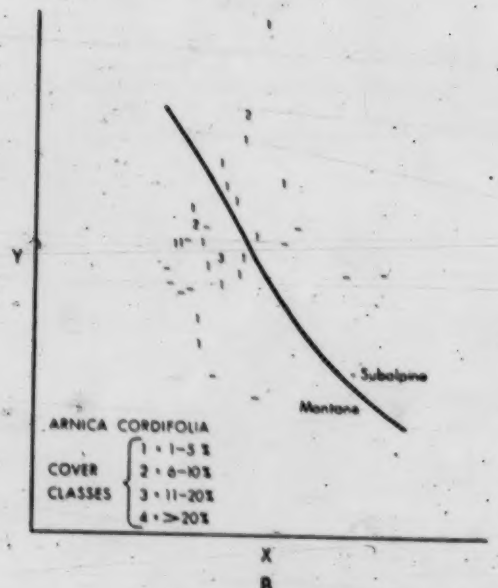

Y
Subalpine
Montane
LINNAEA BOREALIS
COVER CLASSES
1 = 1-5%
2 = 6-10
3 = 11-20
4 = >20
X
D

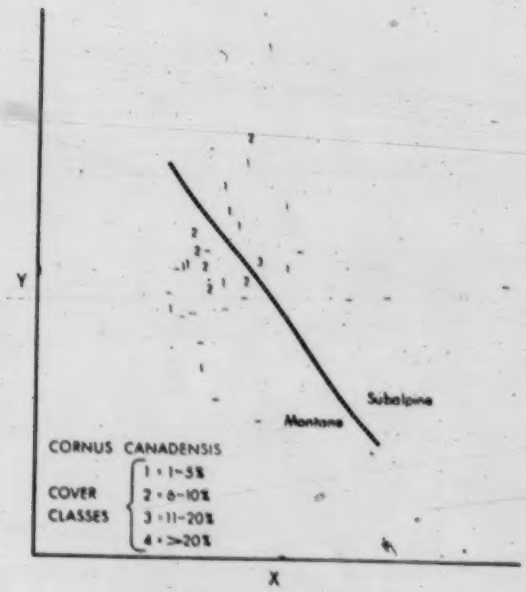
Figure 20. Cover class pattern of *Elymus innovatus* (A); *Arnica cordifolia* (B), *Cornus canadensis* (C) and *Hylocomium splendens* (D) on the ordination field.


Y
X
Subalpine
Montane
ELYMUS INNOVATUS
COVER CLASSES
1 = 1-5%
2 = 6-10%
3 = 11-20%
4 = >20%

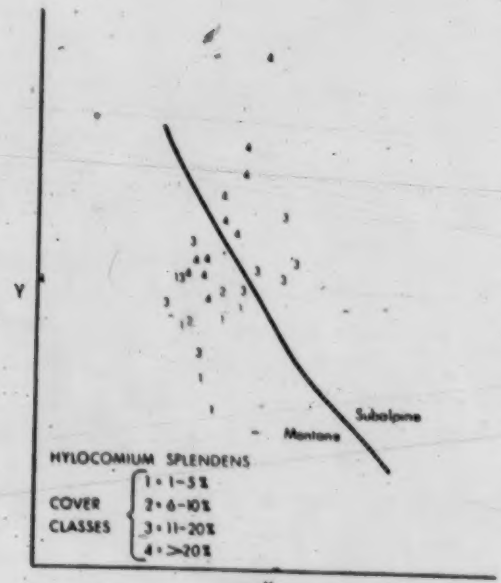
A


Y
X
Subalpine
Montane
ARNICA CORDIFOLIA
COVER CLASSES
1 = 1-5 %
2 = 6-10%
3 = 11-20%
4 = >20%

B


Y
X
Subalpine
Montane
CORNUS CANADENSIS
COVER CLASSES
1 = 1-5%
2 = 6-10%
3 = 11-20%
4 = >20%

C


Y
X
Subalpine
Montane
HYLOCOMIUM SPLENDENS
COVER CLASSES
1 = 1-5%
2 = 6-10%
3 = 11-20%
4 = >20%

D

highly negatively correlated ($r = -.95$, $p < 0.01$), but both occurred together in the *Au - Cp* as well as the *Pm/Je/Cp* h.t. (Table 14). *C. purpurascens* was more abundant under a canopy cover *(P. menziesii)* whereas *A. uva-ursi* had higher cover in the scrub community.

Arnica cordifolia was fairly widespread in distribution, but was primarily confined to the *Picea-Abies* and *Picea glauca* Series, and appears to be an indicator of mesic forest types (Fig. 20). Much the same affinity was indicated by *Hylocomium* distribution, with the highest cover values associated mainly with *Picea-Abies* Series or the more mesic h.t.s of the *Picea glauca* Series. *Vaccinium scoparium* was not widely distributed being confined mainly to the lower elevation of the *Pe-Al/Mg-Vm* h.t., especially the burned portion. *V. scoparium* distribution was associated with the more xeric stands of the *Picea-Abies* Series, and in this instance, sandy loam soils.

As with many other variables a number of understory attributes were related directly or indirectly to stand maturity. Both *Linnaea borealis* and *Arnica cordifolia* were significantly correlated with basal area and ages of some tree species, whereas *Arctostaphylos uva-ursi* was more abundant in both open and non-forested communities (Table 14). *Hylocomium splendens* was positively related to *P. menziesii* dominance (basal area, canopy cover) and to the more mature stands of the h.t.s, and was no doubt an influential factor in the high positive correlation between moss cover and stand ages (Tables 14 & 15).

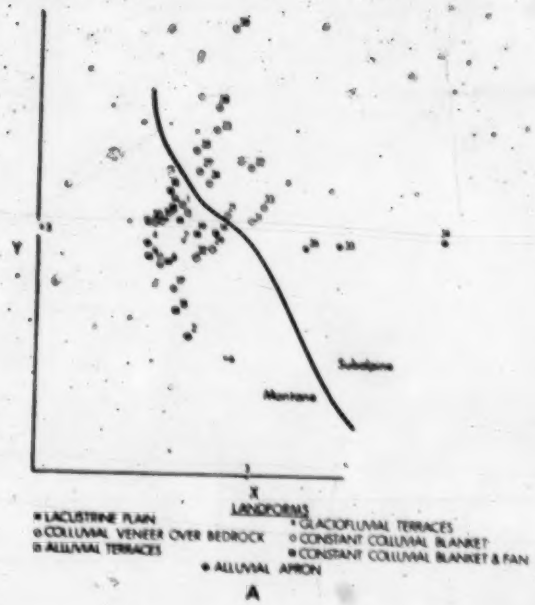
2. Environmental Relationships

No distinct pattern of landforms was exhibited by the ordination since a number of other physical factors were apparently operative in community distribution (Fig. 21A). Stands of the *Picea-Abies* Series occurred most often on the constant colluvial slope, which is a function of landform occurrence in relation to elevation.

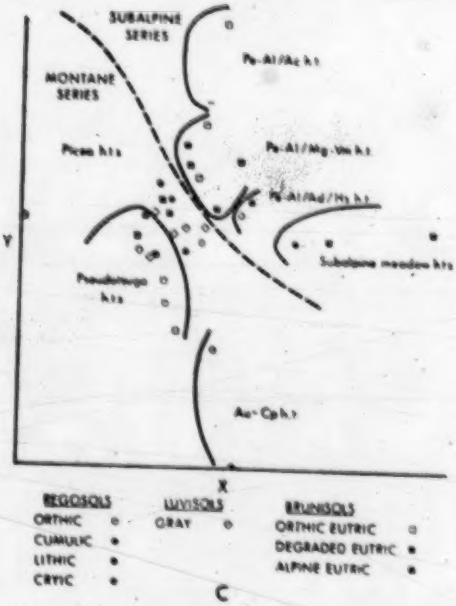
The *Picea* Series contained h.t.s on alluvium of fans and terraces, being at the lowermost basin elevations, as well as others occurring higher on the colluvial slope. Stands associated with glaciofluvial terraces and lacustrine plains were quite distinct on the ordination (Fig. 21A). Stands of both of these landform types did not vary as much in elevation and topographic position which appeared to be quite influential in h.t. differentiation. A large portion of the stands (60%) were on the colluvial blanket landform which covered a wide range of topographic conditions.

A slope exposure index (SEI) was used to help assess the relationship between topography and the ordination pattern: SEI = degree slope x (degree aspect from N/2). Thus, both variables had equal weight in calculating the index which could attain a value of 8100 (90 x 90). Values ranged from 0 (stand 1) to 2211 (stand 32) with the higher numbers indicating, potentially, a more xeric, warmer environment within the range of slope steepness in the basin (to 33°). The indices were plotted according to several classes on Figure 21B.

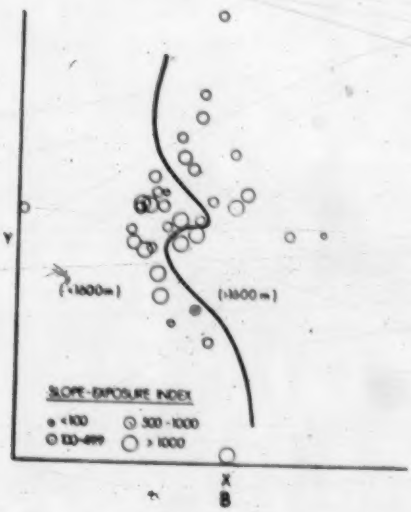
Figure 21. Ordination pattern of landform type (A), topography (B) and soil type (C).


Y
X
Subalpine
Montane
LANDFORMS
LACUSTRINE PLAIN
COLLUVIAL VENEER OVER BEDROCK
ALLUVIAL TERRACES
GLACIOFLUVIAL TERRACES
CONSTANT COLLUVIAL BLANKET
CONSTANT COLLUVIAL BLANKET & FAN
ALLUVIAL APRON

A


SUBALPINE SERIES
MONTANE SERIES
Y
X
Subalpine meadow h.t.s
REGOSOLS
ORTHIC
CUMULIC
LITHIC
CRYIC
LUVISOLS
GRAY
BRUNISOLS
ORTHIC EUTRIC
DEGRADED EUTRIC
ALPINE EUTRIC

C


Y
X
(<1600m)
(>1600 m)
SLOPE-EXPOSURE INDEX
<100
100-499
500-1000
>1000

B

Due to the geologic nature of the basin and erosion processes, slopes were generally steeper at the higher elevations. Stands of the *Pseudotsuga* and *Picea-Pinus albicaulis* h.t.s had the highest SEI values. *P. glauca* h.t.s were quite variable since they occurred over a wide topographic range, but in general had lower index values than stands in the *Pseudotsuga* Series although no statistical significance was indicated ($t = 0.36$, $p > 0.05$).

The importance of slope and aspect in delimiting h.t.s apparently decreases with increase in elevation since much of the subalpine forest was quite uniform in spite of topographic variation. However, very steep S-exposed areas including the *P-Pa/Jc/Ei* h.t. were quite depressed on the ordination field in relation to the elevation gradient (Fig. 21B).

In general, a xeric to mesic gradient can be identified diagonally across the ordination from lower left to upper right on the basis of topography and elevation. This conforms to the climatic data where the *Pe-Al/Ac* (stand 28) and *Sg/Ei* (stand 26) h.t.s exhibited the wettest and coolest environments. Such gradients on ordination fields are quite common although the direction may vary (Maycock & Curtis 1960, Gauch & Whittaker 1972, Stringer 1973).

Using simple correlation analysis, several soil variables appeared to be related to vegetational attributes (Table 15). Soil pH of the A horizon was positively related to the number of species per stand, total tree density and percent standing dead trees. Free lime ($CaCO_3$) was positively related to herb and low shrub cover.

Table 15. Simple correlation between vegetation attributes and environmental variables
Observations ranged from 11 to 18, the reduction being due to the absence of trees in s
at 1% level and * at 5% level.

		1	2	3	4	5	6	7	8	9	10	11	12
Elevation (m)	1	.	.	.	.	.	.	.	.	.	.	.	.
° Slope	2	+.37	.	.	.	.	.	.	.	.	.	.	.
Degrees from S	3	+.01	-.11	.	.	.	.	.	.	.	.	.	.
% Sand	4	-.72**	-.41	-.19	.	.	.	.	.	.	.	.	.
% Clay	5	+.45	+.40	+.17	-.80**	.	.	.	.	.	.	.	.
% Tree-tall shrub cover	6	-.29	+.27	+.26	-.14	-.06	.	.	.	.	.	.	.
% Herb-low shrub cover	7	+.35	+.02	-.01	+.07	+.12	-.58*	.	.	.	.	.	.
% Moss cover	8	-.05	-.11	+.01	+.31	-.32	+.47*	-.37	.	.	.	.	.
% Lichen cover	9	+.23	+.29	-.02	+.11	-.10	+.22	+.06	+.44	.	.	.	.
Number of spp./stand	10	-.26	-.24	-.06	+.44	-.25	+.15	-.04	+.46	-.22	.	.	.
Total tree density	11	-.32	-.22	+.05	+.40	-.24	+.14	+.14	+.40	-.25	+.93**	.	.
Total seedling density	12	+.05	-.01	+.09	+.05	-.06	+.53	-.43	+.38	+.68**	-.30	-.23	.
Relative % dead stems	13	-.31	-.28	-.12	+.46	-.26	+.07	+.02	+.45	-.27	+1.0**	+.93**	-.30
Average R.D.I.[1]	14	+.24	+.26	+.34	-.63	+.56	+.14	+.24	-.46	+.16	-.57	-.48	+.07
Soil Reaction - A horizon	15	-.24	-.13	-.03	+.44	-.26	+.16	-.10	+.42	-.26	+.95**	+.86**	-.31
Soil Reaction - B horizon	16	-.76**	-.12	-.13	+.51	-.11	+.06	+.12	-.34	-.49	+.32	+.30	-.29
Free lime - A horizon	17	-.52	+.27	-.39	+.41	-.19	+.52	-.07	+.35	+.27	+.24	+.38	+.47
Free lime - B horizon	18	-.34	+.52	-.38	+.19	-.06	+.95**	-.21	+.37	+.71	+.22	+.25	+.47
N_2 - A horizon	19	+.68*	+.34	+.04	-.30	+.15	-.45	+.79**	-.32	+.26	+.01	+.23	-.35
N_2 - B horizon	20	+.27	-.11	-.72*	+.07	-.02	+.06	-.50	+.55	+.73*	+.06	+.04	+.49
K - A horizon	21	-60	-.44	+.16	+.37	-.18	+.08	-.00	-.19	-.12	-.79	-.04	+.20
K - B horizon	22	-.82**	-.59	-.16	+.85**	-.58	-.11	-.05	+.01	-.50	+.59	+.50	-.42
Effective Stand Age (ESA)	23	+.29	-.04	-.27	+.09	-.26	+.35	-.32	+.85**	+.24	+.46	+.38	+.04

[1] R.D.I. - Relative diameter increase (mm)

between vegetation attributes and environmental variables from 18 stands in which soils were chemically analyzed.
to 18, the reduction being due to the absence of trees in some stands, and thus significance is indicated by **
5% level.

6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
-.58*																
+.47*	-.37															
+.22	+.06	+.44														
+.15	-.04	+.46	-.22													
+.14	+.14	+.40	-.25	+.93**												
+.53	-.43	+.38	+.68**	-.30	-.23											
+.07	+.02	+.45	-.27	+1.0**	+.93**	-.30										
+.14	+.24	-.46	+.16	-.57	-.48	+.07	-.57									
+.16	-.10	+.42	-.26	+.95**	+.86**	-.31	+.95**	-.71								
+.06	+.12	-.34	-.49	+.32	+.30	-.29	+.30	-.02	+.35							
+.52	-.07	+.35	+.27	+.24	+.38	+.47	+.24	-.01	+.12	+.41						
+.95**	-.21	+.37	+.71	+.22	+.25	+.47	+.17	-	+.29	+.58	+.76*					
-.45	+.79**	-.32	+.26	+.01	+.23	-.35	+.28	+.52	+.01	+.13	-.49	-.04				
+.06	-.50	+.55	+.73*	+.06	+.04	+.49	+.07	-.07	+.15	-.04	-	-.33	-.21			
+.08	-.00	-.19	-.12	-.79	-.04	+.20	-.11	+.06	-.15	+.53	+.21	+.06	-.30	-.33		
-.11	-.05	+.01	-.50	+.59	+.50	-.42	+.58	-.61	+.55	+.68*	+.04	-.13	-.16	-.06	+.50	
+.35	-.32	+.85**	+.24	+.46	+.38	+.04	+.47	-.38	+.36	-.00	-.34	-.41	+.12	+.41	-.43	+.04

(mm)

V

etween vegetation attributes and environmental variables from 18 stands in which soils were chemically analyzed. 18, the reduction being due to the absence of trees in some stands, and thus significance is indicated by ** % level.

6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
-.58*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
+.47*	-.37	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
+.22	+.06	+.44	.	.	.	.	.	.	.	.	.	.	.	.	.	.
+.15	-.04	+.46	-.22	.	.	.	.	.	.	.	.	.	.	.	.	.
+.14	+.14	+.40	-.25	+.93**	.	.	.	.	.	.	.	.	.	.	.	.
+.53	-.43	+.38	+.68**	-.30	-.23	.	.	.	.	.	.	.	.	.	.	.
+.07	+.02	+.45	-.27	+1.0**	+.93**	-.30	.	.	.	.	.	.	.	.	.	.
+.14	+.24	-.46	+.16	-.57	-.48	+.07	-.57	.	.	.	.	.	.	.	.	.
+.16	-.10	+.42	-.26	+.95**	+.86**	-.31	+.95**	-.71	.	.	.	.	.	.	.	.
+.06	+.12	-.34	-.49	+.32	+.30	-.29	+.30	-.02	+.35	.	.	.	.	.	.	.
+.52	-.07	+.35	+.27	+.24	+.38	+.47	+.24	-.01	+.12	+.41	.	.	.	.	.	.
+.95**	-.21	+.37	+.71	+.22	+.25	+.47	+.17	- -	+.29	+.58	+.76*	.	.	.	.	.
-.45	+.79**	-.32	+.26	+.01	+.23	-.35	+.28	+.52	+.01	+.13	-.49	-.04	.	.	.	.
+.06	-.50	+.55	+.73*	+.06	+.04	+.49	+.07	-.07	+.15	-.04	-	-.33	-.21	.	.	.
+.08	-.00	-.19	-.12	-.79	-.04	+.20	-.11	+.06	-.15	+.53	+.21	+.06	-.30	-.33	.	.
-.11	-.05	+.01	-.50	+.59	+.50	-.42	+.58	-.61	+.55	+.68*	+.04	-.13	-.16	-.06	+.50	.
+.35	-.32	+.85**	+.24	+.46	+.38	+.04	+.47	-.38	+.36	-.00	-.34	-.41	+.12	+.41	-.43	+.04

mm)

2 of 2

Significant correlations were not often evident when using soil nutrients as a variable. Of the soil nutrients analyzed, nitrogen and potassium levels appeared to be most correlated (Table 15). Nitrogen of either the A or B horizon was positively related to herb and low shrub and moss cover. Potassium level of the B horizon was positively related to the number of species per stand and negatively with elevation.

Fire history was clearly an important factor in many of the biotic - abiotic relationships, although significant correlation was not often indicated when stand age (ESA) was used as a variable (Table 15). Potassium and pH were positively associated with more recently burned stands as measured by increases in the number of species per stand, percent standing dead trees and RDI (relative diameter increase); note negative correlation between ESA and RDI, Table 15. Free lime levels were usually lower in the older stands which often had more mature soils, or in the case of the glacial cirque *(Sg/Ei & Sv/Pa)* h.t.s, were influenced by drainage from adjacent limestone talus.

Brunisolic soils were the predominant type in the drainage basin, being identified in 18 of the 35 stands (Fig. 21C). Conditions conducive to a Brunisolic profile included a stable landform (the lower section of the colluvial blanquet and fan, and lacustrine plain) and a relatively long time since reaching stability.

Soil Orders showed a definite pattern on the ordination, but no definite pattern was indicated between Soil Subgroups and h.t.s (Fig. 21C).

Geomorphological features were often quite variable within a single h.t. as was indicated by the numerous associated landforms (Table 13, p. 163). Relationships were stronger at the more comprehensive level of the Soil Order, at least among the *Picea-Abies* h.t.s which contained mostly Brunisols. Other h.t.s showing some stand constancy to soil type included the *Au - Cp* and *P - Pa/Jc/Ei* with Regosols, and the *Pm/Jc/Cp* and *Sv - Pa* with Brunisols. As with many other parameters, the *Picea* and *Pseudotsuga* Series exhibited the most variability, containing soils of all three orders (Fig. 21C). Brunisols were the dominant developmental soil type in the *Pseudotsuga* Series, whereas both Brunisols and Luvisols were of nearly equal frequency in the *Picea* Series. Regosols were associated with bedrock or portions of the colluvial blanquet landform on the slopes and ridges, as well as on alluvial terrace and glaciofluvial terrace landforms on the valley floor. Thus the order was quite widespread within the Series (Fig. 21C).

Nutrients, especially N and P were quite low throughout the stands (Appendix 5). No pattern was observed between nutrient values and h.t.s. Instead, many of the mature stands (7, 26, 27, 30) contained the higher N and P values whereas younger stands were higher in K. The higher N and P values and near-climax stands were also associated with soil development with the Brunisolic Order predominating.

VI DISCUSSION AND CONCLUSIONS

A. RELATIONSHIPS OF VINE CREEK H.T.S TO PLANT COMMUNITIES OF OTHER AREAS

The associations described for the Vine Creek drainage basin show certain affinities to communities of other areas, especially within the Rocky Mountain region.

Close comparions of the h.t.s with communities of other areas are difficult since different classification systems are sometimes used, and quantitative data on species' abundance are not always available. Therefore, the degree of relationship between a particular community is necessarily estimated quite subjectively. A distinction between relatively close and more distant relationships was attempted, and two classes are indicated on Table 16. One would expect the degree of relationship (floristic similarity) to weaken with degree of geographic separation.

1. Montane Scrubland

The *Arctostaphylos uva-ursi - Calamagrostis purpurascens* h.t. has not been described as such elsewhere. However affinities exist between this h.t. and the xeric *Koeleria cristata - Calamagrostis montanensis* Grassland described by Stringer (1973) for Jasper and Banff (Table 16). Grass species (*K. cristata, C. montanensis, Agropyron dasystachyum* and *Bromus pumpellianus*) were most abundant in this latter type, whereas *C. montanensis* was quite sparse and *Juniperus communis* and *Rosa acicularis* were more common in the *Au-Cp* h.t. This h.t. is probably more xeric

Table 16. A comparison of other studies with communities similar to the Vine Creek h.t.s. The degree of similarity to assess since various methods and nomenclature were used. Studies having communities that appear simila relationship is uncertain, are indicated by (x), whereas studies describing communities that appear to be are indicated by x. Dashes indicate that a comparison was not applicable.

Authors	Scrubland	Pseudotsuga Series		Picea glauca (intermediate) Series					Picea
	Auu-Cp	Pm/Jc/Cp	Pm/Ei	Pg/Cv-Lb	Pg/Lb/Hs	Pg/Ei-Cc	P(i)/Alc/Ei	P(i)-Pa/Jc/Ei	Pi
Stringer 1973 Jasper N.P.	(x)	-	-	-	-	-	-	-	
Daubenmire 1953 N. B.C.	x	-	-	-	x	-	-	-	
Douglas 1974 S.W. Yukon	x	-	-	-	-	-	-	-	
Hnatiuk 1969 Jasper N.P.	-	(x)	-	(x)	-	(x)	x	-	
Stringer & La Roi 1970 Jasper N.P.	-	x	x	-	-	-	-	-	
Ogilvie 1963 Banff N.P.	-	(x)	-	-	-	-	-	-	
Tisdale & McLean 1957 S. central B.C.	-	(x)	-	-	-	-	-	-	
Illingworth & Arlidge 1960 central B.C.	-	(x)	-	-	-	-	-	-	
Brayshaw 1965 S. B.C.	-	(x)	-	-	-	-	-	-	
McLean 1970 S. B.C.	-	(x)	-	-	-	-	-	-	
Daubenmire & Daubenmire 1968 E. Idaho	-	(x)	-	-	-	-	-	-	
Habeck 1967 W. Montana	-	(x)	-	-	-	-	-	-	
Patten 1963 N. Wyoming	-	(x)	-	-	-	-	-	(x)	
Despain 1973 N. Wyoming	-	(x)	-	-	-	-	-	-	
Lewis 1917 Banff N.P.	-	-	-	-	x	-	-	-	
Ogilvie 1962, 69 Banff N.P.	-	-	-	x	(x)	-	-	-	
Kuchar 1973 Waterton N.P.	-	-	-	-	-	(x)	-	x	
[illegible] 1972 Banff N.P. - S.W. Alta.	-	-	-	-	-	-	-	x	
Moss 1955 W. Alta.	-	-	-	-	x	-	-	-	
Horton 1956 W. Alta.	-	-	-	-	-	x	-	-	
Pogue 1946 central B.C.	-	-	-	-	x	-	-	-	
Wali & Krajina 1973 Interior B.C.	-	-	-	-	x	-	-	-	
Pfister et al. N. Montana	-	-	-	x	x	-	-	(x)	
Habeck 1969 N.W. Montana	-	-	-	-	-	-	-	(x)	
Achuff 1974 N. Alta.	-	-	-	-	x	(x)	-	-	
Mackenzie-Grieve 1970 N. central Alta.	-	-	-	-	-	-	x	-	
Corns 1972 N.W. Alta.	-	-	-	-	-	-	x	-	
Duffy 1964 N.W. Alta.	-	-	-	x	-	-	-	-	
Lee 1965 N.W. Alta.	-	-	-	x	-	-	-	-	
Bell 1966 Jasper-Banff N.P.	-	-	-	-	-	-	-	-	
Horton 1959 W. Alta.	-	-	-	-	-	-	-	-	
Cormack 1956 S.W. Alta.	-	-	-	-	-	-	-	-	
Cooper 1916 W. B.C.	-	-	-	-	-	-	-	-	
Smith 1955 central B.C.	-	-	-	-	-	-	-	-	
Eady 1971 central B.C.	-	-	-	-	-	-	-	-	
Oosting & Reed 1952 S. central Wyoming	-	-	-	-	-	-	-	-	
Langenheim 1962	-	-	-	-	-	-	-	-	

comparison of other studies with communities similar to the Vine creek h.t.s. The degree of similarity is often difficult to assess since various methods and nomenclature were used. Studies having communities that appear similar, but where the relationship is uncertain, are indicated by (x), whereas studies describing communities that appear to be strongly related are indicated by x. Dashes indicate that a comparison was not applicable.

crubland	Pseudotsuga Series		Picea glauca (intermediate) Series					Picea engelmannii - Abies lasiocarpa Series		
Auu-Cp	Pm/Jc/Cp	Pm/Ei	Pg/Cv-Lb	Pg/Lb/Hs	Pg/Ei-Cc	P(i)/Alc/Ei	P(i)-Pa/Jc/Ei	Fe-Al/Mg-Vm	Fe-Al/Ac	Fe-Al/Ad/Hs
(x)	-	-	-	-	-	-	-	-	-	-
x	-	-	-	x	-	-	-	-	-	-
x	-	-	-	-	-	-	-	-	-	-
-	(x)	-	(x)	-	(x)	x	-	x	x	(x)
-	x	x	-	-	-	-	-	-	-	-
-	(x)	-	-	-	-	-	-	x	-	-
-	(x)	-	-	-	-	-	-	-	-	-
-	(x)	-	-	-	-	-	-	-	-	-
-	(x)	-	-	-	-	-	-	-	-	-
-	(x)	-	-	-	-	-	-	-	-	x
-	(x)	-	-	-	-	-	-	x	-	-
-	(x)	-	-	-	-	-	-	x	-	-
-	(x)	-	-	-	-	-	(x)	-	(x)	-
-	(x)	-	-	-	-	-	-	-	(x)	-
-	-	-	-	x	-	-	-	-	-	-
-	-	-	x	(x)	-	-	-	x	-	-
-	-	-	-	-	(x)	-	x	x	-	-
-	-	-	-	x	-	-	-	x	-	-
-	-	-	-	-	x	-	-	-	-	-
-	-	-	-	x	-	-	-	-	-	-
-	-	-	-	x	-	-	-	-	-	-
-	-	-	x	x	-	-	(x)	x	(x)	(x)
-	-	-	-	-	-	-	(x)	-	-	-
-	-	-	-	x	(x)	-	-	x	-	-
-	-	-	-	-	-	x	-	-	-	-
-	-	-	-	-	-	x	-	-	-	-
-	-	-	x	-	-	-	-	-	-	-
-	-	-	x	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	x	(x)	-
-	-	-	-	-	-	-	-	x	x	-
-	-	-	-	-	-	-	-	x	-	-
-	-	-	-	-	-	-	-	x	-	-
-	-	-	-	-	-	-	-	x	-	-
-	-	-	-	-	-	-	-	-	-	x
-	-	-	-	-	-	-	-	-	x	-
-	-	-	-	-	-	-	-	-	x	-

than that represented by the *Koeleria - Calamagrostis* Grassland, being on steeper slopes with S exposures. The relatively high abundance of *A. uva-ursi, Solidago decumbens, Artemesia frigida* and *Koeleria cristata* is indicative of heavy grazing (Stringer 1973) and a zootic influence is probably important, along with warm xeric mesoclimate in maintaining this association.

The h.t. may be more common in areas of the Rocky Mtns to the N of the study area. Douglas (1974) recognized a *Juniperus communis - Arctostaphylos uva-ursi* community in SW Yukon which seems similar to the *Au-Cp* h.t. However, the northern community was designated as seral to a *Picea glauca - Shepherdia canadensis* community and the Vine Creek h.t. was considered a topo-zootic climax. Daubenmire (1953) reported a similar community for N British Columbia.

Scrub types are not uncommon along the lower elevations of the montane zone within the Rocky Mountains and often occur between grassland and forest vegetation. Kuchar (1973) described a prairie shrubland *(Amelanchier & Symphoricarpos)* for Waterton N.P., and noted that it is quite similar to the *Festuca - Danthonia* grassland of the area. The lower grassland zone of Spilsbury and Tisdale (1944) in S British Columbia, and the widespread sagebrush community type described by Daubenmire (1956) in N Idaho, by Reed (1952) and Despain (1973) in Wyoming, and Langenheim (1962) in W central Colorado are in the same general vegetation zone as the *Au-Cp* h.t. named here. Grass *(viz. Koeleria cristata, Agropyron trachycaulum, Stipa* spp., *Bromus* spp.) is associated with the more dominant shrubs in all these areas.

2. *Pseudotsuga* H.T.s

The *Pseudotsuga menziesii/Juniperus communis/Calamagrostis purpurascens* association shows some affinity to the *P. menziesii/Calamagrostis rubescens* association that has been described in Jasper and Banff N.P., and frequently in other areas of the N Rockies of the U.S. Stringer and La Roi (1970) described a *Pseudotsuga/Calamagrostis - Elymus* association in Jasper and Banff, and noted that *Juniperus communis* was an important associate as was *Elymus innovatus*. *Calamagrostis rubescens* occurred very infrequently in the Vine Creek stands. Hnatiuk (1969) described a xerophytic *Pinus contorta* forest that also appears related to the h.t. *Shepherdia canadensis* was more abundant than *J. communis* and *Calamagrostis* spp. were not noted. Hnatiuk thought that the successional trend was toward *P. menziesii* at these xeric sites, but commented that regeneration was very slow and lodgepole dominance was presently being maintained.

The *Pm/Calamagrostis rubescens* association of south central B.C. also shows some relationship to the *Pm/Jc/Cp* h.t. of Vine Creek. Both *Linnaea borealis* and *A. uva-ursi* were listed as important species for the association by Tisdale and McLean (1957). However, *Juniperus communis* is replaced by several other shrub species in S British Columbia and N Idaho. McLean (1970) described the association as containing *Rosa gymnocarpa* and *Spiraea betulifolia*, whereas Brayshaw (1965) listed *Salix bebbiana* as an understory component, and in contrast to some of the other descriptions, did not list *A. uva-ursi*. Illingworth and Arlidge (1960) noted *A. uva-ursi* in their *Calamagrostis* Site Type near Prince George, but it was not a major species.

Daubenmire and Daubenmire (1968) observed that stands of this association in N Idaho contained virtually no shrub stratum and *Calamagrostis rubescens* and *Carex* spp. essentially formed the understory. An *A. uva-ursi* phase of this association was recognized for a section of Idaho near the Canadian border (Daubenmire & Daubenmire 1968); and apparently is consistent with findings in S British Columbia (Brayshaw 1965, Illingworth & Arlidge 1960) as well as in Banff (Ogilvie 1963). Although *A. uva-ursi* was present in the Vine Creek h.t., it was sometimes secondary in importance, which was also observed in the general vitinity by Stringer and La Roi (1970).

The *P. menziesii* forest of the Big Horn Mtns, Wyoming appears to be more remote in relationship, although *J. communis* was the dominant shrub at the lower part of the elevation range (Despain 1973). No other constant, unifying species were identified for the Wyoming type, although some grasses (*Hesperochloa* & *Poa* spp.) were also important in the understory.

The *P. menziesii/Elymus innovatus* association of Jasper (Stringer & La Roi 1970) is apparently not as widespread as the *Pm/Cr* h.t. It appears closely related to the stands in the Vine Creek basin having *Linnaea borealis*, *Aster conspicuus*, *Hylocomium splendens* and *Peltigera canina* as important understory species in addition to *E. innovatus*. However, *Juniperus communis* was not listed as a major shrub in the earlier study, and *Arctostaphylos uva-ursi* and *Fragaria virginia* were not always abundant in the Vine Creek area.

Hnatiuk (1969) described an *Elymus innovatus* type for the *P. contorta* forest in the Jasper area, but the type was found to be quite heterogeneous, and it was thought by Hnatiuk to be intermediate to more xeric *Arctostaphylos* and more mesic *Shepherdia* types.

Stringer and La Roi (1970) found the *Pm/Cr - Ei* association, which was not prominent in Jasper, at a higher equivalent elevation than the *Pm/Ei* association. The *Pm/J. communis/C. purpurascens* association in the Vine Creek basin occurred at a lower elevation than the *Pm/Ei* association indicating a more xeric h.t. However, the *Pm/Ei* h.t. was usually on steeper slopes, often with S-aspects.

The presence and dominance of *Elymus innovatus* distinguish the *Pm/Ei* association from a number of other *P. menziesii* associations, including those in the interior of B.C. (Stringer & La Roi 1970). These authors postulated that the Jasper associations may have evolved from the *Pseudotsuga/Calamagrostis* association of British Columbia, and that it has diverged under a boreal, continental influence.

3. *Picea glauca* and *P. glauca* x *engelmannii* H.T.s

Montane *Picea glauca* forests of Jasper and Banff N.P. have heretofore not been as intensively studied as most of the other forest types in the two parks. The boreal *P. glauca* forests in the Alberta foothills and N British Columbia have been more extensively described. Some floristic affinities are expected between the forest types in the boreal and Rocky Mountain portions of Alberta because of their geographic proximity (Moss & Pegg 1963, Ogilvie 1962).

The *Pg/Carex vaginata - Linnaea borealis* h.t. does not appear to be widespread in the Rocky Moutains (Table 16). Pfister *et al.* (1974) described a *Picea/Equisetum* h.t. for N Montana which has some floristic similarity. As in the present study, their association occurred on lowlands and alluvial valley bottoms. The h.t. is equated with the *Picea/Equisetum* h.t. of Ogilvie (1962) for the Banff area. Although *Equisetum (E. pratense)* was not as dominant in the Vine Creek basin, it exhibited aspect dominance in some of the depressional areas of the h.t. This fact, and the presence of *Cornus stolonifera, Galium triflorum, Cornus canadensis* and *Smilacina stellata* indicate a fairly close affinity. The association in Banff and N Montana did not contain *Amelanchier alnifolia* or *Linnaea borealis* as major understory components, however. The *Pg/Equisetum* association appears quite commonly in Jasper N.P. and the Foothills (G. H. La Roi pers. comm., Duffy 1964, Lees 1965). Hnatiuk (1969) described a stand within the "Mesophytic Lodgepole Pine Forest Class" in Jasper that contained *C. vaginata* as well as other herbaceous wetland species.

Picea glauca forests with a dominant *Linnaea borealis* understory appear to be quite widespread (Table 16). Communities resembling the *Pg/L. borealis/Hylocomium splendens* h.t. have been described both to the N and S of the study area in the Rockies, to the E in boreal Alberta and to the NW in N British Columbia. Lewis (1917) characterized "deep valley floors" near Banff as containing *P. glauca* with a thick moss *(Ptilium crista-castrensis)* understory which also contained *L. borealis*. Moss (1955) described a general type, which although variable in understory,

contained *L. borealis* and a thick *Hylocomium* carpet. His Cordilleran Association appears to contain a number of h.t.s, and probably includes the *Pg/Cc - Lb* as well as the *Pg/Lb/Hs* associations listed here.

The community described by Lewis (1917) is probably similar to those described by Ogilvie (1962) and Kirby and Ogilvie (1969) for Banff N.P. However, *Cornus canadensis*, which was only infrequently abundant in the Vine Creek stands, was listed as the associate of *Hylocomium* giving a *Picea/Cc - Hs* h.t. in the Banff area.

Communities similar to the *Pg/Lb/Hs* h.t. have been described in British Columbia (Wali & Krajina 1973) especially in the northern portion, and it probably extends into the S Yukon. Pogue (1946) noted that a "green moss", and subordinate species including *L. borealis* and *C. canadensis* occurred in N central British Columbia in mature forests. Pogue's description indicates that this type is similar to the *P. glauca* forb-rich forest of Daubenmire (1953) which was described further N near the British Columbia - Yukon border. Some floristic differences do occur between the more northern area and Vine Creek. Pogue (1946) listed *Tiarella, Clintonia* and *Streptopus* as minor associates, none of which were observed in the Vine Creek h.t.

Achuff (1974) recognized a *Cornus - Linnaea* community in NW Alberta for the boreale *Picea - Abies* forest which appears similar in some respects to the Vine Creek h.t. However, Achuff listed *Viburnum edule* and *Lonicera involucrata* as prominent members of the shrub stratum.

These species only occurred in the mature stands of the Vine Creek h.t. and then as minor components of the understory. Examination of the above literature indicates a strong boreal concentration for the *Pg/Lb/Hs* h.t. Yet, Pfister *et al.* (1974) delimited a *Picea/L. borealis* h.t. for N Montana on cool, well-drained benches. Other associates in their h.t., including *Vaccinium* spp., indicate a higher elevation than that represented in the Vine Creek basin.

Published references to an *Elymus innovatus - Cornus canadensis* dominated understory beneath *P. glauca* in the Rockies are not common. Hnatiuk (1969) recognized an "*Elymus* nodum" of the Mesophytic Lodgepole Pine Forest in Jasper. However, *Cornus canadensis* was not abundant in this type which otherwise contained a similar flora to the Vine Creek *Pg/Ei/Cc* h.t. Regeneration of *P. glauca* or *P. engelmannii* was present, but was quite variable. La Roi *et al.* (1975) described a similar type for Jasper N.P. in the vicinity of Pyramid and Signal Mtns. Horton (1956) designated a "High Foothills" division for the lodgepole pine forest of Alberta which appears to encompass Hnatiuk's *Elymus* forest type. A number of dominant species *(Elymus, Linnaea, Cornus canadensis)* are quite ubiquitous, making it difficult to compare communities. Kuchar (1973) designated a *C. canadensis* type for the lower spruce-fir forest in Waterton N.P. However, *E. innovatus* was not an associate, and the presence of a number of other species *(Equisetum arvense, Carex capillaris, Cornus stolonifera, Lonicera involucrata)* indicate that this and the Vine Creek h.t. are not closely related.

A *Cornus - Linnaea* community type was recognized by Achuff (1974) for the spruce-fir forest in NW Alberta. He noted that this was intermediate to several other community types, having a non-distinct floristic composition. The important presence of *Viburnum edule, Lonicera involucrata, Aralia nudicaulis* and *Rubus* spp., and the absence of *Elymus innovatus* indicate that this and the *Pg/Ei/Cc* h.t. of Vine Creek are not closely related.

The *Pg-Pi/Alnus crispa/E. innovatus* h.t. does not appear to be common in the Rockies (Table 16, p. 200). Hnatiuk (1969) recognized an *Alnus crispa* type for the lodgepole pine forests of Jasper and Banff N.P. This type appears to be similar to the Vine Creek h.t. in many respects, but *Vaccinium scoparium*, a prominent species in Hnatiuk's type, was quite sparse in the present study. Also, regeneration of *Abies lasiocarpa* in the Vine Creek h.t. was more limited than in Hnatiuk's type. Moss (1955) in his review does not designate an *Alnus* spp. faciation for either the lodgepole pine or white spruce associations, although *Alnus crispa* is noted as an important shrub in the Alberta foothills and subalpine forests. Corns (1972) described an *Alnus* type during regeneration of lodgepole pine forests after logging in the foothills near Edson, but the degree of relationship is difficult to discern. Mackenzie - Grieve (1970) recognized a *Pinus - Picea/Alnus - Hylocomium* vegetation type for the foothills in central Alberta which exhibits a close affinity to the h.t. described here. Differences include the dominance of *Calamagrostis canadensis, Epilobium angustifolium, Rubus pubescens*, and *Stenanthium occidentale*, and the low

abundance of *Rosa acicularis* in the foothill stands. Understory similarities include an abundance of *Arnica cordifolia, Elymus innovatus, Cornus canadensis* and *Linnaea borealis* in addition to *Hylocomium splendens*.

The *Picea - Pinus albicaulis/Juniperus communis/E. innovatus* h.t. appears to be quite common on wind-exposed ridges in the N and far-N Rocky Mountains. Moss (1955) described a limber pine *(P. flexilis)* rocky ridge vegetation as a general type for this habitat in the Alberta Rockies. Baig (1972) in a more intensive study of this zone, recognized a number of similar associations. His *P. albicaulis - Picea - Abies/ Juniperus communis* h.t. appears to have the greatest affinity with the Vine Creek association. Similar communities have also been described in Waterton N.P. and in N Montana. Kuchar (1973) recognized a fir/whitebark pine h.t. on dry ridges near timberline in Waterton N.P. which appears more similar to the *Abies (Pinus albicaulis)/Vaccinium scoparium* h.t. described by Pfister *et al.* (1974) for N Montana. Although the above associations appear to occupy similar habitats, major understory species including *Xerophyllum tenax, Hieracium gracile* and *Carex geyeri* did not occur in the Vine Creek area. Both of these types appear somewhat similar to Daubenmire's (1952) *Picea - Abies/Xerophyllum tenax* h.t. for N Idaho and NE Washington which was also described by Ogilvie (1963) in the Crowsnest area of Alberta (Kuchar 1973). Habeck (1969) recognized a similar h.t. in Glacier, Montana.

P. albicaulis extends into N central Wyoming where it forms high elevation forests with *Picea engelmannii* and *Abies lasiocarpa* (Despain

1973). Apparently *A. lasiocarpa* is more important than *P. engelmannii* as a codominant of the forest h.t. in the more S areas of the Rockies. *P. albicaulis* is sometimes viewed as a long-lasting seral species (Pfister *et al.* 1974) and appears to produce an environment conducive to *A. lasiocarpa* regeneration after fires on rocky wind-exposed slopes (Day 1967, Habeck 1967). *P. albicaulis* establishment was observed to occur more readily amoung clumps of *Juniperus communis* and/or *Arctostaphylos uva-ursi* on the more barren ridges in the present study.

4. *Picea - Abies* H.T.s

The *Picea engelmannii - Abies lasiocarpa* subalpine forest has received considerable attention in the N portion of the Rocky Mountains, probably due to its potential importance to the forest industry. The *Pe-Al/Menziesia glabella - Vaccinium membranaceum* h.t. is relatively widespread in the N Rockies and easily recognized by the shrub union (Table 16, p. 200). Beil (1966) described spruce-fir community types for the Banff - Jasper area that exhibit an affinity to the h.t., although the dominance of *Vaccinium scoparium* and *Salix drummondii* in some of his stands indicates some variance. Hnatiuk (1969) observed a similar type and noted the lower abundance of *V. scoparium* under the taller *Menziesia - Rhododendron* stratum. He also recognized a high subalpine *V. scoparium* type, but this was confined to Banff N.P. The h.t. is probably the equivalent of the moist *P. engelmannii* type of Horton (1959), although this encompasses a fairly broad section of the subalpine spruce-fir forest. Cooper (1916) recognized what appears to be a similar type in the Mt Robson area of W British Columbia. However, *Cassiope* and

Phyllodoce were listed as components, and are usually indicative of higher elevation flora in Jasper N.P.

Cormack (1956) described a similar type in the Crowsnest Pass area of Alberta, but in this case the S location is indicated by the dominance of *Pachystima myrsinites*.

Ogilvie (1963) and Kirby and Ogilvie (1969) in Banff, and Pfister *et al.* (1974) in NW Montana recognized both *Menziesia* and *V. scoparium* types. The dominance of *Xerophyllum tenax* distinguishes a southern affiliate to this h.t. Kuchar (1973) noted this in Waterton N.P. although *Menziesia, Arnica cordifolia* and *V. membranaceum* were strongly represented in his stands. Habeck (1967) and Pfister *et al.* (1974) also noted the tendency for *Xerophyllum* to form a union with *Menziesia*. Further west in Idaho, *Menziesia* and *Xerophyllum* have been designated as indicating mesic and more xeric h.t.s respectively (Daubenmire & Daubenmire 1968).

Smith (1955) designated a *Menziesia - Rubus pedatus* spruce-fir forest type for central British Columbia. This appears to be similar to Achuff's (1974) *Rubus pedatus/Ptilium* community type for the boreal spruce-fir in NW Alberta. *R. pedatus* was sparse in the Vine Creek h.t.

The *Pe-Al/Arnica cordifolia* h.t. is not well represented in the two parks in the literature. *Arnica cordifolia* has a wide geographic range in the Rocky Mountains which complicates making comparisons of equivalent h.t.s. The high cover of *A. cordifolia, Pyrola secunda* and constance of

Lycopodium annotinum indicate that Beil's (1966) study included stands similar to the *Pe-Al/Ac* h.t. Horton (1959) and Hnatiuk (1969) also described similar communities. Although *Arnica cordifolia* was present in a number of *Abies* types in SW Alberta and NW Montana, it is usually of secondary importance to a number of other species. However, *Arnica* again becomes important in descriptions further south in Montana, and in Wyoming and Colorado. Pfister *et al.* (1974) recognized an *Abies/Arnica cordifolia* association, which although not closely related to that in the Vine Creek basin, occurred in a relatively mesic environment on limestone parent material. Descriptions of areas further S do not indicate this degree of relationship, although the spruce-fir forest is similarly low in number of understory species. *Ribes* spp. often occur as the only component of a medium shrub stratum and a dense moss carpet is usually described (Oosting & Reed 1952, Langenheim 1962, Patten 1963, Despain 1973). Interestingly, *Vaccinium scroparium* is again a strong associate of the subordinate strata in all of the above studies. Langenheim (1962) noted that this species was more common in the eastern Colorado Rockies, and occurred primarily on the higher, but drier slopes in the Gunnison, Colorado area in the western part of the state.

A spruce-fir association containing *Arnica diversifolia* as a diagnostic component is not well recognized *(Pe-Al/Ad/Hylocomium splendens* h.t., Table 16). Hnatiuk (1969) described a mesic subalpine *Hylocomium splendens* type for Jasper, but *A. diversifolia* was not observed. High, mesic subalpine stands of Beil (1966) also do not show a strong affinity to this h.t. However, a *Phyllodoce empetriformis* phase of the *Abies* -

Vaccinium scoparium h.t. described by McLean (1970) and Eady (1971) in south central British Columbia appears somewhat similar, although containing a more dominant low shrub *(Vaccinium scoparium)* stratum. A herb component of *Arnica latifolia* and *Valeriana sitchensis* compares favorably with the Vine Creek h.t., and also occurs near timberline. Pfister *et al.* (1974) described a similar h.t. for NW Montana, although the presence of *Pinus albicaulis* and *Hieracium gracile* detract from indicating a close relationship. This h.t. was similarly near timberline.

5. Subalpine Scrub and Meadow H.T.s

Subalpine meadows and scrublands are common, although usually restricted in area, throughout the central and northern portions of the Rocky Mountains (Reed 1952, Daubenmire 1953, Moss 1955, Langenheim 1962, Patten 1963, Stringer 1973). Communities similar to the *Salix glauca/ Elymus innovatus* h.t. have been described in Banff and the near-by Front Range by Beder (1967) and Trottier (1972). *Betula glandulosa* and *Elymus innovatus* occurred as major associates of *Salix glauca* in subalpine stream-sides in Banff, probably an equivalent h.t. of the *Salix barratiana* association described by Trottier. However, Beder (1967) also described a *S. barratiana* association, but on steep ravine banks near creeks. Common species for these areas and the Vine Creek h.t. include *Senecio indecorus, S. triangularis, Deschampsia caespitosa, Trollius albiflorus* and *Valeriana sitchensis*. Flook (1964) described a similar h.t. for moist valley bottoms of the Jasper area.

Communities similar to the *Sg/Ei* h.t. have been recognized in areas further south, often as a *Salix* - grass association, which has been described as a *Salix* thicket community in S Montana (Johnson & Billings 1962), and W central Wyoming as a shrub-swamp community (Reed 1952). Patten (1968) also recognized a *Salix* community near streams in N Wyoming which occurs within the *Artemesia tridentata* zone.

Communities similar to the Vine Creek h.t. have also been described in the mountains to the N. Raup (1947) described a subalpine scrub for the Mackenzie Mtn Range in the Northwest Territories in which *Salix glauca*, *Betula glandulosa* and *Festuca altaica* were dominants. Daubenmire (1953) recognized a subalpine scrub community in the W Yukon and S Alaska area which appears somewhat similar. However, *Betula glandulosa*, *Empetrum nigrum*, *Phyllodoce glandulifera* and *Cassiope tetragona* were major associates of the h.t. in these areas. Douglas (1974) described a *Picea glauca* - *Betula glandulosa* - *Empetrum nigrum* community in SW Yukon as a mesic climax type of his "montane zone".

Subalpine meadows have been described under a variety of names. Lewis (1917) recorded a mat herbage community of *Poa alpina*, *Festuca brachyphylla* for the Banff area which appears similar to the *Salix vestita/Poa alpina* h.t. delimited here. Hrapko (1970) recognized a *Salix arctica* - *Arctagrostis arundinacea* community on Signal Mtn in Jasper N.P. which appears somewhat similar floristically, but was definitely alpine. Similar types have also been described by Beder (1967) in Banff N.P. and by Trottier (1972) in the Front Range SE of

Banff. These communities are often designated as representing wet, mesic habitats within either the alpine or subalpine zone. The species composition of the h.t. is variable, although some (*Salix vestita, S. nivalis, Erigeron peregrinus, Poa alpina, Phleum alpinum, Trisetum spicatum, Luzula* spp.) are quite constant throughout the literature. Other studies delimiting similar types include Kuchar's (1973) moist forb community in Waterton N.P. (although *Salix* was not a dominant), the *Poa, Koeleria, Agrostis* subalpine meadows of Habeck (1967) in Glacier N.P., Montana, the sedge-grass meadow community of Reed (1952) in W central Wyoming, and the upland herb community noted by Langenheim (1962) in W central Colorado. The last community is of special interest since a number of its important species (*Phleum alpinum, Calamagrostis purpurascens, Agropyron trachycaulum, Festuca brachyphylla*) also occur in the Vine Creek h.t.s.

6. Miscellaneous H.T.s

Although a number of other communities in the Vine Creek basin were of very limited extent and not studied in detail, several of those recognized do appear in the literature, but their floristic and quantitative relationships cannot be assessed very closely. *Dryas octapetala* dominated alpine tundra is widespread in the Jasper area forming a number of alpine community types (Kuchar 1975). Hrapko (1970) described *Dryas* - lichen and *Dryas* - *Salix arctica* communities which seem quite similar to those observed here. Trottier (1972) recognized a *D. octapetala* association on exposed ridges which appears similar, although some floristic differences between areas are notable. Especially

germane is the *D. octapetala -Oxytropis podocarpa* association delimited by Beder (1967) in Banff. This community occurred on gentle, wind-exposed slopes and has a flora similar to that of alpine communities on the Gargoyle-Redan ridges in the Vine Creek basin.

Hangmoor peatlands or mountain bogs have been described in a number of areas, but especially to the north of the study area. Moss (1955) noted the community type in referencing Crossley (1951) who discussed conditions conducive to mountain bog formation. Laidlaw (1971) recognized a *Tomenthypnum* stand group in his study of the *P. mariana* vegetation in Jasper and Banff N.P.; which appears to be closely related to communities observed here. Analagous species include *Ledum groenlandicum, Betula glandulosa, Carex aquatilis* and *Sphagnum warnstorfii*. This community appears to have a northern affinity, resembling those described for N British Columbia and the Yukon (Raup 1947, Porsild 1951, Daubenmire 1953). Wali and Krajina (1973) described a *P. mariana - Sphagnum - Betula pumila* bog community in NE British Columbia and noted its boreal affinity.

Several papers have made reference to the avalanche h.t.s of the Alberta Rockies. Stringer (1973) mentions an *Elymus innovatus* shrub savanna for Banff N.P. that resembles the Vine Creek avalanche chute flora at relatively low elevations, and on steep S or SW-exposed slopes. The avalanche meadows described by Trottier (1972) west of High River, Alberta are somewhat similar to those of the higher areas of the basin, containing *Valeriana sitchensis, Achillea millefolium, Fragaria virginiana* and a number of grasses *(Phleum, Poa, Bromus, Trisetum)*.

The open *Populus tremuloides* parkland h.t. is a variant of Moss' (1932) Parkland vegetation type of central Alberta, and contains elements of the "Northern Prairie" *(Koeleria, Agropyron, Solidago)* as well as shrubs *(Rosa, Shepherdia, Elaeagnus)* which represent a prairie-poplar ecotone. This community was not extensive in Vine Creek and, as indicated by Moss (1955) for many of the poplar types in the Alberta Rockies, appears seral to *Picea glauca*.

B. GEOGRAPHIC RELATIONSHIPS OF THE VINE CREEK FLORA

The floristic composition of the basin changes from predominantly boreal to predominantly Cordilleran elements with increase in elevation. Species generally regarded as northern include those of the lower montane h.t.s (e.g., *Picea glauca, Linnaea borealis, Geocaulon lividum, Cornus canadensis, Elymus innovatus)* especially those of the *Picea glauca* Series (Moss & Pegg 1963, Achuff 1974). Although there was no clear-cut distinction between the floristic affinities of the montane *Pseudotsuga* and *P. glauca* stands, certain Cordilleran species *(Calamagrostis purpurascens, Spiraea lucida)* appear mainly in the former. However, *Juniperus communis, Arctostaphylos uva-ursi* and *Elymus innovatus* may represent northern elements within the *Pseudotsuga* communities (Hultén 1968, Habeck 1972). These species were primarily associated with the montane h.t.s in the Vine Creek basin.

Species having either Cordilleran or Pacific affinities are more frequent in the subalpine *Picea - Abies* meadow h.t.s. Some of these

include *Arnica cordifolia, Anemone parviflora, A. richardsonnii, Thalictrum occidentale, Parnassia fimbriata, Veratrum eschscholtzii, Menziesia glabella* and *Rhododendron albiflorum* (Moss & Pegg 1963). A number of other species of the *Picea - Abies/Arnica diversifolia/Hylocomium splendens* and subalpine shrub meadow h.t.s seem be be Cordilleran on the basis of occurrence in the Rocky Mountain community descriptions in Montana, Wyoming and Colorado, and Hultén's (1968) range maps. These include *Festuca brachyphylla, Trisetum spicatum, Phleum alpinum, Arnica diversifolia, A. mollis, Juncus drummondii* and *Carex atrosquamea*. Flora of Banff and especially Waterton N.P. is mainly Cordilleran and seems to contain fewer boreal elements than Jasper (Ogilvie 1962, Kuchar 1975).

C. VEGETATION PATTERN IN THE VINE CREEK DRAINAGE BASIN

The distribution of different plant communities in the basin were; (1) not perfectly correlated with physiographic features, (2) not the simple outcome of fire history, (3) not the simple outcome of biological interaction, and (4) were not totally random. Rather communities appeared to fall within limits determined by a combination of physiographic, historic, interactive and stochastic factors. Therefore each community has its own "realized niche' (*sensu* Hutchinson 1965) within its fundamental "niche space" afforded to it by the basin at the time of the study. The fundamental "niche spaces" of the communities within the basin are thus realized with the distribution of its "habitat type" *sensu* Daubenmire (1968a). This relationship between plant community distribution and a complex of environmental variables was most evident as a vegetation mosaic within the elevational and topographic ranges of the drainage basin.

Alpine, subalpine and montane zones are the major divisions of the vegetation, ranging from the upper to the lower elevations of the drainage basin. These zones correspond to different, but intergrading macroclimates and follow a general gradient from xeric-warm to moist-cool which corresponds to elevation increase. Similar trends have been found in numerous studies of the Rocky Mountain vegetation, including those in Jasper N.P. (Beil 1966, Hnatiuk 1969, Stringer & La Roi 1970). Each zone would appear to have a specific array of h.t.s.

In this study, distinct assemblages of stable vegetation associations have been used as indicators of h.t.s. These h.t.s are considered by Daubenmire (1952) as "the basic ecological units of the landscape". However, as expressed by Daubenmire and Daubenmire (1968), complex fire history makes the interpretation of habitat types difficult in most of the Rocky Mountains and, "vegetation of disturbed areas is highly variable,...even on a relatively uniform type of habitat", since "competitive elimination has not had time to provide the closest relationship between the vegetation and environment".

1. Succession

Fires have been the most important agent in succession - climax relationships in the study area. The montane zone has had a complex fire history and consists mostly of subclimax forest communities, whereas the subalpine zone contained mostly mature near-climax communities ("climax" is here defined as a relatively stable, self-maintaining community *sensu* Whittaker 1953). The relatively complex pattern of the montane communities is related to fire frequency, as well as variable successional rates on different h.t.s.

A number of significant fires in the Vine Creek drainage basin appear to have been widespread in the N Rocky Mountains. Larsen (1925), Habeck (1972) and Houston (1973) also note the 1870, 1890-1895, 1910 and 1919 dates as periods of major fires in the Rocky Mountain area of N Idaho and Montana. The complex age structure of the *Pseudotsuga menziesii* h.t.s is due to a large number of *P. menziesii* trees surviving fires

since about 1895, and a lesser number of trees surviving fires since about 1700. The *Picea glauca* h.t.s were burned differentially by the 1870, 1910 and 1919 fires. Stands in glaciofluvial coves and on river alluvium and fans near Jasper Lake have somehow escaped burning since about 1800, and stands near the open *Au-Cp* shrubland h.t. usually contained scarred, pre-fire relict individuals of *P. menziesii*. The ability of *P. menziesii* to survive fires which apparently destroyed any existing *Picea glauca* and *Pinus contorta* is an important factor in the present complexity of the vegetation mosaic. Another factor is the apparent ability of *P. menziesii* to occur as a seral species, along with *P. contorta*, in the more mesic *P. glauca* h.t.s. Habeck (1963) noted that *P. menziesii* often occurs as a subclimax species in the *Thuja-Tsuga* forest in W Montana. The importance of *P. menziesii* in the *P. glauca* h.t.s declined with elevation and was minimal in the *Pg/Alc/Ei* association. Although *P. menziesii* and *P. glauca* tend to be segregated toward warm, dry and cool, mesic habitats respectively (Krajina & Brooke 1970), the existence of codominant climax communities has also been recognized for the Douglas fir forest subzone in B.C. and for the N Rocky Mountains in general (Daubenmire 1943, McLean & Holland 1958). *P. menziesii* and *P. glauca* sometimes appeared together as self-maintaining populations (*viz.* stands 5 & 9). Daubenmire (1969) discussed the possibility that *P. menziesii* may be a survivor of the old "Temperate Mesophytic Forest" - only suited to a thin zone between the "Montane Taiga" and "Xerophytic Forest". However, *P. menziesii*, in the absence of *Pinus ponderosa*, forms the xerophytic forest in relation to the mesic habitat preference of *P. glauca* in the study area.

The burned area of the subalpine *Picea - Abies* forest was quite obvious due to the homogeneous nature of adjacent, mature communities at higher elevations. A stepwise progression of tree establishment occurred in this area following the last major fire (ca 1910). *P. contorta* was followed by *P. engelmannii (P.* intermediate) establishment after about a 15 year interval. *Abies lasiocarpa* regeneration has been much slower with many of the trees establishing about 30 years after the fire. This progression is similar to the "pine to spruce" successional trend described by Cormack (1953). On the N exposed slope of this subalpine area, however, *P. contorta* did not establish as well as *Picea*. This pattern is similar to Cormack's (1953) "spruce and pine to climax" succession. *P. contorta* appeared to establish from 5 to 10 years after the fire on the N exposure. As found by Stahelin (1943), the rate of events following fire varies with site conditions, and *P. contorta* establishment was apparently slower on the cooler, N exposures.

The 1910 burn also has a significant, long-lasting effect on the *P-Pa/Jc/Ei* association which is still visually dominated by standing snags in some parts of the h.t. A similar feature was observed by Habeck (1972) on the higher ridges in an area of NW Montana. Forests in the 1910 burn area continue to have significantly lower tree biomass (basal area) values than those of the surrounding unburned area, and lower values than reported earlier for similar forests of both N.P.s (Beil 1966, Hnatiuk 1969, Stringer & La Roi 1970).

The codominance of *P. engelmannii* and *A. lasiocarpa* is well recognized as a major feature of the subalpine zone, but the climax status of the two species apparently varies. Evidence of self-maintenance of both species was ample in the Vine Creek h.t.s. The reproductive potential of *A. lasiocarpa* appeared to increase with elevation, however, while that of *P. engelmannii* decreased. Beil (1966) observed the tendency of *A. lasiocarpa* to layer at the higher elevations, whereas *P. engelmannii* did not. He concluded that the two species were able to co-exist because of different niche requirements and life history patterns; a view supported here. The differences in the two are possibly illustrated by the relatively high number of *Abies* seedlings, which are offset by a high mortality and shorter life span in relation to those of *P. engelmannii*. *A. lasiocarpa* is apparently more sensitive to fire but more shade tolerant than *P. engelmannii* (Daubenmire & Daubenmire 1968, Wellner 1970). These traits probably account for *P. engelmannii* to be more restricted in distribution in areas with higher precipitation and fewer fires (e.g. coast) leaving *A. lasiocarpa* as the sole climmax dominant in many western subalpine forest associations (Daubenmire & Daubenmire 1968, Franklin & Dyrness 1973, Pfister *et al.* 1974).

The patterns of understory species are easier to assess in relation to fire history. The understory floristic composition was usually not strikingly different in h.t.s containing subclimax and near-climax stands. Dyrness (1973) noted that most of the original understory in a *Pseudotsuga* forest in W Oregon had returned after only 5 yrs after burning. The observation of Daubenmire and Daubenmire (1968) that the

"forest and undergrowth occupy the land independently" is germane to observations here. The burned section of the *Pe-Al/Mg-Vm* h.t. had an understory very similar to those of the more mature stands which had a predominance of "key" climax species listed by Cormack (1956). The regeneration of a climax understory is thus a relatively rapid process (Lyon 1971). This fact limits their usefulness in successional interpretations of the drainage basin but enhances their values as indicators of the h.t.s or "site types" (*sensu* Cajander 1926). A number of species which Cormack (1956) designated as seral (*Antennaria* spp., *Fragaria* spp., *Aster* spp., *Arctostaphylos uva-ursi*, legumes) were not important in the subalpine h.t.s except in avalanche chutes. Similarly, some species that are important members of climax communities in the Montane (e.g. *Pseudotsuga menziesii, Shepherdia canadensis, Elymus innovatus, Linnaea borealis)* are important only in certain seral communities in the Subalpine. Many of these same species were important on stable sites at lower elevations and on steep, S exposed slopes at higher elevations, and are considered good indicators of montane h.t.s. Thus the successional niches of many wide-ranging understory, as well as tree species, varies with h.t. in the Vine Creek basin. This was discussed by Daubenmire and Daubenmire (1968) as a major point for using relatively stable communities as indicators of a h.t.

2. Influences of the Physical Environment

A number of relationships between the distributions of communities and environmental factors became obvious during the study.

The relationship between particular landforms and h.t.s was not strong. The continuous nature and broad elevational range encompassed by some landforms (e.g. colluvial slopes) probably accounts for the inclusion of several h.t.s in a single landform. A finer textural landform classification system could help in discerning a closer correlation between the colluvial slope landform and h.t.s. Pettapiece (1971) utilized land units within a mountain slope land system which took into account slope steepness and aspect. Although some of these smaller units contained several communities, correspondence between landform and the equivalent of the Series used here was obtained in his analysis.

Conversely, a number of h.t.s in the lower montane occurred on several landforms, due in part to the topographic complexity of what McPherson (1970) described as "ice stagnation" terrain. The correspondence between h.t. and landforms was thus easier to perceive in this lower zone. *P. glauca* h.t.s were primarily associated with the alluvial terraces and glaciofluvial coves, whereas those of *Pseudotsuga* were associated with glaciofluvial ridges and especially the more upland colluvial slopes. This habitat segregation between the two species has been observed in a number of other areas of the Rocky Mountains (Le Barron & Jemison 1953, McLean & Holland 1958, Ogilvie 1969, Stringer & La Roi 1970, Wali & Krajina 1973). The steep S exposures of the glaciofluvial terraces always contained the xerophytic *Au-Cp* scrubland h.t. at the lower elevation of the drainage basin.

No close relationship was evident between h.t.s and soil Subgroups. Soil Orders were associated mainly with the distribution of the larger vegetation Series. Most Regosols and all Luvisols occurred on h.t.s in the montane Series; Brunisols occurred in both the montane and subalpine zones, but mainly in the *Picea - Abies* h.t.s. Pettapiece (1971) concluded that soil and forest types are usually not strongly correlated, especially if the area has a history of recent fires. The constancy of Brunisols within the mature *Picea - Abies* h.t.s supports the disruptive influence that fire has on the maturation of a particular soil type. Daubenmire and Daubenmire (1968) also concluded that few correlations could be discerned between soil classes and h.t.s since "plant roots are sensitive to moisture, solutes and temperature, whereas soil classification is based on characters to which the human eye is sensitive". Clearcut correlations between vegetation and soil types have been observed elsewhere however. Patten (1963) and Despain (1973) found good agreement between soil and vegetation patterns in N Wyoming, probably due to distinct differences in parent material. Nimlos and McConnell (1965), although noting a close landform - soil relationship, did not observe the same degree of affinity between soil and vegetation. McLean (1970) found that some h.t.s were well correlated with soil, but at the great group level, a trend also observed in this study. Pettapiece (1971) observed that parent materials high in carbonate content inhibit the depth of Regosols. This is pertinent to the soils on the ridges as well as those on alluvial sites at lower elevations. High pH and percent sand values were common on the latter sites in the basin.

Soil nutrient content varied most with fire history; soils of the younger stands usually were higher in K content. Available nutrients are generally thought to increase after fires (Ahlgren & Ahlgren 1960, Wright & Heinselman 1973) which convert biomass and soil litter to ash. However, N especially can easily be lost by volitization and erosion processes during and after burning (Lutz 1956). Wagle and Kitchen (1972) observed higher available soil N and P values in non-burned areas and old burns compared to areas having a more recent (3 yr) fire history. The increase in nutrient content of the surface or near surface horizons with age may be due to the accumulation of organic material, and thus a lower total available nutrient pool. The low N and P nutrient regime of Regosols in general, and the fact that none of the stands have been burned recently makes it difficult to detect definite soil-nutrient trends in the drainage basin.

Climatic variables, although assessed with a modest network of stations, show the strongest correlations with h.t. distributions. The climatic gradient generally followed the elevational gradient, but other topographic variables were important in changing gradient steepness. This is in accordance with the observations of Geiger (1950) and Daubenmire (1968b) on the influence of mountain topography on local climate.

The elevation - temperature gradient of the drainage basin (ca $-1^{o}C$ $100\ m^{-1}$) is steeper than that reported by Spilsbury and Tisdale (1944) for an area in S British Columbia ($-0.9^{o}C$ $100\ m^{-1}$) and also for mountain areas in general (Oosting 1956; - $0.5^{o}C$ $100\ m^{-1}$ increase). Depressional

areas (glaciofluvial coves) and plateaus had lower temperatures than adjacent slopes. Within the subalpine zone, these areas were quite distinct containing shrub and meadow communities. Pockets of cold air also occurred behind physical barriers (e.g. ridges perpendicular to the main valley, forest boundaries), as described by Geiger (1950).

The decrease in temperature with elevation increase is paralleled by an increase in precipitation (+2 cm, 100 m^{-1}). Precipitation - elevation gradients in other parts of the Cordilleran do not appear as steep (Patten 1963, Despain 1973). However, the problems associated with the accurate measurement of precipitation and its variable distribution pattern limit the usefullness of relating the gradient to plant-community occurrence.

Soil moisture was an important variable in h.t. differentiation. The driest late-summer soil conditions were found in the montane scrubland. Soil moisture of *Pseudotsuga*, *Picea glauca*, and *Pinus contorta (Pg/Alv/Ei)* sites was quite similar, and usually greater than that of the montane scrubland site. The alpine tundra site was relatively xeric, although not showing the degree of stress or variability observed at some of the lower elevation sites. The steep slope and rocky substratum increased the aridity of the alpine site, since precipitation was relatively high. Soil moisture was neither as variable nor limiting in the subalpine zone, being relatively abundant throughout the zone.

Many of these relationships of vegetation zones and h.t.s with climatic variables are in accordance with other workers. Larsen (1930) noted in N Idaho and Montana that lower elevation communities require high temperature and less moisture than those of higher zones. Daubenmire (1943b) and Spilsbury and Tisdale (1944) arrived at similar conclusions for areas in N Idaho and S British Columbia, where soil moisture was deemed to be the most influencial factor at lower elevations, whereas temperature and length of frost-free period were more important in the higher vegetation zones. Daubenmire (1956) observed that heat deficiency is important in restricting *Pinus ponderosa* and *Pseudotsuga menziesii* to the lower zones in E Washington and N Idaho. In his later work in the same area, Daubenmire (1968b) found a close correlation between climax communities and soil moisture regimes. Siccama (1974) has observed quite steep climatic gradients between zonal vegetation as compared to those within a particular zone. The Vine Creek weather stations were not numerous enough to pinpoint such interzonal "breaks" in the climatic gradient.

The subalpine zone of the basin has a cool, mesic climate which, except for cold-air drainage pockets and snow basins, is apparently quite uniform over a relatively large area. The montane zone has a more diverse array of climates and thus a larger number of h.t.s.

It is concluded that the Vine Creek drainage basin is a moderately well-organized system of interacting abiotic and biotic factors, the totality of which is expressed very well by the repeating patterns of

the plant communities that collectively form its vegetation. The distribution and importance of these plant communities in relation to each other and to larger mountain landscape systems are by no means unique to the study area; they seem to be valid for a much larger area along the east slope of the Canadian Rockies. Other basins in Jasper National Park should be investigated to test this hypothesis and to better understand the function of these landscape systems toward better management.

VII. SUMMARY

1. The vegetation of the Vine Creek drainage basin, Jasper National Park was studied in order to ascertain certain relationships between plant community distribution and environmental factors within a mountain landscape system. Quantitative data were collected from 35 stands, while qualitative data were collected from additional sites, in order to designate plant communities. The stands were grouped into habitat types, indicating climax communities using cluster analysis, two-dimensional ordination and tree regeneration statistics.

2. The physical features of the drainage basin were investigated by dividing the landscape into ridge, valley slope and valley floor landform complexes. Landform nomenclature included information on soil parent material as an aid to interpretation of soil and community/relationships. Colluvial blanket was by far the most abundant landform, covering most of the slope complex. Although till is exposed in some of the lower elevations of the basin, colluvial deposition has masked many of the glacial features.

3. In general, a warm-dry to cool-wet climatic gradient followed elevation increase. The upper stations had over twice the amount of precipitation than that observed at the lower elevations of the basin; a gradient followed by a decrease in temperature. However, the steepness of the gradient was affected by local variation in

topography (e.g. depressional areas were affected by cold air drainage and basin discharge, whereas steep S exposed slopes were conversely drier due to increased insolation and rapid drainage). This differential in gradient steepness was reflected by the vegetation mosaic. Subalpine meadow and *Picea glauca* communities were related to cold air drainage basins, and montane scrubland and some *Pseudotsuga menziesii* communities were associated with steep S exposures. This habitat type separation was reflected by temperature, and to some degree soil moisture data. However, soil compaction, texture, elevation and community physiognomy were important factors in producing a soil moisture regime. The subalpine *Picea - Abies* forest site had the most mesic soil moisture regime which varied little through the growing season.

4. Thirteen habitat types were identified from the stand data. These represented two main elevation zones, the montane and subalpine. Five Series were identified within these two zones indicating variation within major climatic gradients. Eight habitat types were identified in the montane zone, including; *1)* montane scrubland *(Arctostaphylos uva-ursi - Calamagrostis purpurascens), 2) Pseudotsuga menziesii/Juniperus communis/Calamagrostis purpurascens, 3) Pm/Elymus innovatus, 4) Picea glauca/Carex vaginata - Linnaea borealis, 5) Pg/L. borealis/Hylocomium splendens, 6) Pg/E. innovatus - Cornus canadensis, 7) Pg/Alnus crispa/E. innovatus, 8) Picea - Pinus albicaulis/J. communis/E. innovatus.* Five h.t.s were identified for the subalpine zone, including; *1) Picea engelmannii - Abies*

lasiocarpa/Menziesia glabella - Vaccinium membranaceum, 2) Pe - Al/Arnica cordifolia, 3) Pe - Al/Arnica diversifolia/H. splendens and 4 & 5) the subalpine shrub meadows of *Salix glauca/E. innovatus* and *Salix vestita/Poa alpina*. Other communities of the drainage basin, including *Dryas hookeriana - Oxytropis podocarpa* alpine tundra, rock and lichen tundra, *Populus tremuloides* parkland and forest, *Picea mariana* fen and those of snow and avalanche chutes, were also described.

5. Three Soil Orders; Regosol, Brunisol and Luvisol, were observed in the drainage basin. The Regosols were widespread occurring on bedrock of ridges and on alluvium of the valley floor. Luvisols occurred primarily in the lower portion of the drainage basin and were commonly associated with till. Brunisols were dominant in the subalpine *Picea - Abies* communities, and in some of the near-climax communities within the montane zone. Fluvial and colluvial parent materials were often associated with Brunisolic soils.

6. Community relationship were investigated using two-dimensional ordination and inferences on biotic and abiotic relationships from simple correlations. The stand distribution on the ordination field exhibited an asymptotic arrangement which appeared to conform to a gradient from warm-xeric to mesic to cool-wet. This corresponds to h.t.s on low elevation, steep S exposed slopes of coarse till, to gentle N exposed slopes, to wet depressional lacustrine basins at relatively high elevations. A number of species were associated

with this climatic gradient. *Juniperus communis*, *Arctostaphylos uva-ursi* and *Calamagrostis purpurascens* were associated with the more xeric h.t.s. Others, including *Sherpherdia canadensis*, *Rosa acicularis*, *Alnus crispa*, *Aster conspicuus*, *Linnaea borealis*, *Elymus innovatus*, *Cornus canadensis* and *Hylocomium splendens* had a wider amplitude, being associated with intermediate (mesic) h.t.s. Those mainly associated with the cooler, wetter subalpine h.t.s including *Vaccinium membranaceum*, *Menziesia glabella*, *Ledum groenlandicum*, *Rhododendron albiflorum* and *Arnica cordifolia*. Major species of the subalpine meadows were restricted in distribution, being associated with h.t.s of cool temperatures and wet conditions during summer and deep winter snow.

7. A similar relationship was observed between elevation and geographic affinity. A number of species, and communities of the lower elevations had a boreal affinity, and those at the higher elevations, especially in the subalpine had Cordilleran or Pacific affinity. This relationship is exemplified by a *Picea glauca* - *P. glauca* x *engelmannii* - *P. engelmannii* gradient. *P. glauca* occurred mainly below 1450 m and *P. engelmannii* occurred mostly above 1600 m. However, *P. glauca* characters were extended upward in elevation on S exposed slopes and characters indicating *P. engelmannii* occurred at lower elevations on N exposures.

8. Fires have had a major impact on the montane and lower subalpine vegetation pattern. This is reflected by the mixed composition of many of the forest communities, containing a dominance of *Pinus contorta* with *Pseudotsuga menziesii* and *Picea glauca* occurring often as subordinates. *P. contorta* occurs as a relatively long-lasting subclimax on the more xeric habitats within the *P. glauca* Series. On the more mesic habitats however, *P. contorta* does not appear as important in a seral role, and *Picea* (intermediate & *P. engelmannii)* regenerate somewhat independently of an established tree cover. This relationship is exhibited by a reduction in tree biomass (basal area) on the N exposed slopes of the lower subalpine forest.

9. A number of environmental factors were correlated with stand maturity. In general *Vaccinium membranaceum, Menziesia glabella, Linnaea borealis, Arnica cordifolia* and mosses, especially *Hylocomium splendens,* increased in cover with tree stand age. *Juniperus communis* and *Rosa acicularis* often had high cover in younger stands, but this was not consistent. Increase in the number of species per stand was associated with the more recently burned areas.

10. Although relationships between association, landforms and soil types are not always strong, some patterns were apparent. Analyses indicated that there is a closer correspondence between climax communities and climatic variables, regardless of the variability

of other factors, including those associated with landforms and soils. However, both landforms and soils are helpful in interpreting vegetation pattern, since information concerning substrate and its present form influences mesoclimate. The drainage basin is characterized as a system of interrelated abiotic and biotic components which are expressed by features of the vegetation.

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Appendix 1. Species Identified in the Vine Creek Drainage Basin arranged by Family

VASCULAR

OPHIOGLOSSACEAE

Botrychium lunaria (L.) Sw.

POLYPODIACEAE

Cystopteris fragilis (L.) Bernh.

EQUISETACEAE

Equisetum arvense L.

Equisetum fluviatile L.

Equisetum pratense Ehrh.

Equisetum scirpoides Michx.

Equisetum variegatum Schleich.

LYCOPODIACEAE

Lycopodium annotinum L.

PINACEAE

Abies lasiocarpa (Hook.) Nutt.

Juniperus communis L.

Juniperus horizontalis Moench

Pinus albicaulis Engelm.

Pinus contorta Loudon var. latifolia Engelm.

Picea engelmannii Parry

Picea glauca (Moench) Voss

Picea mariana (Mill.) BSP.

Pseudotsuga menziesii (Mirb.) Franco

GRAMINEAE

Agropyron latiglume (Scribn. & Smith) Rydb.

Agropyron riparium Scribn. & Smith

Agropyron smithii Rydb.

Agropyron trachycaulum (Link) Malte

Agrostis thurberiana Hitchc.

Bromus pumpellianus Scribn.

Calamagrostis canadensis (Michx.) Beauv.

Calamagrostis montanensis Scribn.

Calamagrostis purpurascens R. Br.

Danthonia intermedia Vasey

Deschampsia caespitosa (L.) Beauv.

Elymus innovatus Beal

Festuca brachyphylla Schultes

Hordeum jubatum L.

Koeleria cristata (L.) Pers.

Muhlenbergia cuspidata (Torr.) Rydb.

Phleum alpinum L.

Poa alpina L.

Poa interior Rydb.

Poa pratensis L.

Stipa comata Trin. & Rupr.

Trisetum spicatum (L.) Richt.

CYPERACEAE

Carex aquatilis Wahlenb.

Carex atrosquama Mack

Carex aurea Nutt.

Carex concinna R. Br.

Carex filifolia Nutt.

Carex media R. Br.

Carex nardina Fries

Carex nigricans C.A.Meyer

Carex phaeocephala Piper

Carex retrorsa Schwein.

Carex scirpoidea Michx.

Carex spectabilis Dewey

Carex vaginata Tausch

Carex sp.

Carex umbellata Schk.

Eriophorum brachyantherum Trautv.

JUNCACEAE

Juncus balticus Willd.

Juncus drummondii E. Meyer

Luzula parviflora (Ehrh.) Desv.

Luzula spicata (L.) DC.

Luzula wahlenbergii Rupr.

LILIACEAE

Disporum trachycarpum (S. Wats.) B.&H.

Lilium philadelphicum L. var. andinum (Nutt.) Ker

Smilacina stellata (L.) Desf.

Veratrum eschscholtzii A. Gray

Zygadenus elegans Pursh

IRIDACEAE

Sisyrinchium montanum Greene

ORCHIDACEAE

Calypso bulbosa (L.) Oakes

Corallorhiza trifida Chatelain

Cypripedium calceolus L. var. pubescens (Willd.) Correll

Goodyera oblongifolia Raf.

Habenaria hyperborea (L.) R. Br.

Habenaria obtusata (Pursh) Richards

Listera cordata (L.) R. Br.

Orchis rotundifolia Banks

SALICACEAE

Populus balsamifera L.

Populus tremuloides Michx.

Salix arctica Pall.

Salix barrattiana Hook.

Salix bebbiana Sarg.

Salix glauca L.

Salix planifolia Pursh

Salix pseudomonticola Ball

Salix vestita Pursh

BETULACEAE

Alnus crispa (Ait.) Pursh

Alnus tenifolia Nutt.

Betula glandulosa Michx.

Betula occidentalis Hook.

Betula papyrifera Marsh.

Betula pumila L. var. glandulifera Regel

SANTALACEAE

Comandra pallida A. DC.

Geocaulon lividum (Richards.) Fern.

LORANTHACEAE

Arceuthobium americanum Nutt.

POLYGONACEAE

Oxyria digyna (L.) Hill

Polygonum viviparum L.

PORTULACACEAE

Claytonia lanceolata Pursh

CARYOPHYLLACEAE

Arenaria rubella (Wahlenb.) J.E. Sm.

Cerastium beeringianum Cham. & Schlecht.

Lychnis apetala L.

Silene acaulis L. var. exscapa (All.) DC.

Stellaria longipes Goldie

RANUNCULACEAE

Actaea rubra (Ait.) Willd.

Anemone drummondii S. Wats.

Anemone multifida Poir.

Anemone occidentalis S. Wats.

Anemone parviflora Michx.

Aquilegia flavescens S. Wats.

Caltha leptosepala DC.

Clematis verticellaris DC. var. columbiana (Nutt.) A.Gray

Delphinium glaucum S. Wats.

Ranunculus acris L.

Ranunculus eschscholtzii Schlecht.

Ranunculus pedatifidus J.E. Smith var. affinis (R.Br.) L. Benson

Thalictrum venulosum Trel.

Trollius albiflorus (A.Gray) Rydb.

PAPAVERACEAE

Papaver kluanensis D. Löve

CRUCIFERAE

Arabis divaricarpa A. Nels.

Arabis drummondii A. Gray

Arabis lyallii S. Wats.

Brassica campestris L.

Braya glabella Richards.

Braya humilis (C.A. Mey.) Robins.

Draba nivalis Lilijebl. var. elongata S. Wats.

Draba oligosperma Hook.

Draba paysonii Macbr. var. treleasii (Schulz) C.L. Hitchc.

Physaria didymocarpa (Hook.) A. Gray

SAXIFRAGACEAE

Mitella nuda L.

Mitella pentandra Hook.

Parnassia fimbriata Konig

Parnassia parviflora DC.

Ribes hirtellum Michx.

Ribes hudsonianum Richards.

Ribes lacustre (Pers.) Poir.

Ribes oxycanthoides L.

Saxifraga adscendens L.

Saxifraga aizoides L.

Saxifraga caespitosa L.

Saxifraga cernua L.

Saxifraga lyalli Engler

Saxifraga oppositifolia L.

Saxifraga rhomboidea Greene

Saxifraga tricuspidata Rottb.

Telesonix heucheriformis Rydb.

ROSACEAE

Amelanchier alnifolia Nutt.

Dryas drummondii Richards.

Dryas hookeriana Juz.

Dryas integrifolia M. Vahl

Fragaria virginiana Duchesne

Potentilla diversifolia Lehm.

Potentilla fruticosa L.

Potentilla hyparctica Malte -

Potentilla nivea L.

Rosa acicularis Lindl.

Rosa woodsii Lindl.

Rubus acaulis Michx.

Rubus pedatus J.E.Smith

Rubus strigosus Michx.

Sorbus sitchensis Roemer

Spiraea lucida Dougl.

LEGUMINOSAE

Astragalus aboriginum Richards.

Astragalus alpinus L.

Astragalus frigidus (L.) A. Gray var. americanus (Hook.) S. Wats.

Astragalus striatus Nutt.

Astragalus tenellus Pursh

Hedysarum alpinum L.

Hedysarum boreale Nutt. var. cinerascens (Rydb.) Rollins

Hedysarum mackenzii Richards.

Lathyrus ochroleucus Hook.

Melilotus alba Desr.

Oxytropis campestris (L.) DC.

Oxytropis podocarpa A. Gray

Oxytropis splendens Dougl.

Trifolium pratense L.

Trifolium repens L.

GERANIACEAE

Geranium richardsonii Fisch. & Trautv.

LINACEAE

Linum lewisii Pursh.

ACERACEAE

Acer glabrum Torr.

VIOLACEAE

Viola adunca J.E. Smith

Viola renifolia A. Gray

Viola rugulosa Greene

ELAEAGNACEAE

Elaeagnus commutata Bernh.

Shepherdia canadensis (L.) Nutt.

ONAGRACEAE

Epilobium angustifolium L.

Epilobium hornemannii Reichenb.

Epilobium latifolium L.

UMBELLIFERAE

Osmorhiza chilensis Hook. & Arn.

Osmorhiza purpurea (Coult. & Rose) Suksd.

CORNACEAE

Cornus canadensis L.

Cornus stolonifera Michx.

PYROLACEAE

Moneses uniflora (L.) A. Gray

Pyrola asarifolia Michx.

Pyrola bracteata Hook.

Pyrola grandiflora Radius

Pyrola minor L.

Pyrola secunda L.

Pyrola virens Schweigg.

ERICACEAE

Arctostaphylos rubra (Rehder & Wils.) Fern.

Arctostaphylos uva-ursi (L.) Spreng.

Cassiope mertensiana (Bong.) D.Don.

Cassiope tetragona (L.) D.Don ssp. saxifontana (Small) Porsild

Ledum groenlandicum Oeder

Menziesia glabella A. Gray

Phyllodoce empetriformis (Smith) D.Don

Phyllodoce glanduliflora (Hook.) Coville

Rhododendron albiflorum Hook.

Vaccinium caespitosum Michx.

Vaccinium membranaceum Dougl.

Vaccinium myrtillus L.

Vaccinium scoparium Leiberg

Vaccinium vitis-idaea L.var. minus Lodd.

PRIMULACEAE

Androsace septentrionalis L.

GENTIANACEAE

Gentiana glauca Pallas

Gentianella amarella (L.) Borner ssp. acuta (Michx.) J.M.Gillett

Gentianella propinqua (Richards.) J.M.Gillett

HYDROPHYLLACEAE

Phacelia sericea (Graham) A.Gray

BORAGINACEAE

Lappula echinata Gilib.

Lithospermum incisum Lehm.

Mertensia paniculata (Ait.) G. Don

Myosotis alpestris Schmidt

LABIATAE

Prunella vulgaris L.

SCROPHULARIACEAE

Castilleja miniata Dougl.

Castilleja occidentalis Torr.

Castilleja septentrionalis Lindl.

Pedicularis bracteosa Benth.

Veronica alpina L. var. unalaschcensis C. & S.

OROBANCHACEAE

Orobanche fasciculata Nutt.

LENTIBULARIACEAE

Pinguicula vulgaris L.

PLANTAGINACEAE

Plantago major L.

RUBIACEAE

Galium boreale L.

Galium triflorum Michx.

CAPRIFOLIACEAE

Linnaea borealis L. var. americana (Forbes) Rehd.

Lonicera dioica L. var. glaucescens (Rydb.) Butters

Sambucus pubens Michx.

Symphoricarpos albus (L.) Blake

Viburnum edule (Michx.) Raf.

VALERIANACEAE

Valeriana septentrionalis Rydb.

Valeriana sitchensis Bong.

CAMPANULACEAE

Campanula rotundifolia L.

COMPOSITAE

Achillea millefolium L. ssp. lanulosa (Nutt.) Piper

Agoseris aurantiaca (Hook.) Greene

Agoseris glauca (Pursh) Raf.

Anaphalis margaritacea (L.) Benth. & Hook.

Antennaria alpina (L.) Gaertn.

Antennaria lanata (Hook.) Greene

Antennaria neglecta Greene

Antennaria nitida Greene

Antennaria pulcherrima (Hook.) Greene

Antennaria racemosa Hook.

Antennaria umbrinella Rydb.

Arnica cordifolia Hook.

Arnica diversifolia Greene

Arnica latifolia Bong.

Arnica mollis Hook.

Artemisia campestris L.

Artemisia frigida Willd.

Artemisia norvegica Fries

Aster laevis L.

Aster ciliolatus Lindl.

Aster conspicuus Lindl.

Aster hesperius A. Gray

Aster sibiricus L.

Cirsium foliosum (Hook.) DC.

Crepis tectorum L.

Erigeron caespitosus Nutt.

Erigeron compositus Pursh

Erigeron glabellus Nutt. ssp. pubescens (Hook.) Cronq.

Erigeron humilis Grah.

Erigeron peregrinus (Pursh) Greene

Gaillardia aristata Pursh

Hieracium umbellatum L.

Petasites frigidus (L.) Franch.

Petasites palmatus (Ait.) A. Gray

Petasites sagittatus (Pursh) A. Gray

Saussurea densa (Hook.) Rydb.

Senecio cymbalarioides Nutt.

Senecio indecorus Greene

Senecio pauperculus Michx.

Senecio subnudus DC.

Senecio triangularis Hook.

Solidago decumbens Greene

Solidago multiradiata Ait.

Sonchus arvensis L.

Taraxacum lyratum (Ledeb.) DC.

Townsendia sericea Hook.

Tragopogon dubius Scop.

SPHAGNACEAE

Sphagnum warnstorfii Russ.

DITRICHACEAE

Distichium capillaceum (Hedw.) B.S.G.

DICRANACEAE

Dicranum polysetum Sw.

POTTIACEAE

Tortella tortuosa (Hedw.) Limpr.

Tortula norvegica (Web.) Wahlenb. ex Lindb.

AULACOMNIACEAE

Aulocomnium palustre (Hedw.) Schwaegr.

BARTRAMIACEAE

Philonotis fontana (Hedw.) Brid.

BRYACEAE

Bryum pseudotriquetrum (Hedw.) Gaertn., Meyer & Scherb.

Bryum sp.

Pohlia nutans (Hedw.) Lindb.

THUIDIACEAE

Thuidium abietinum (Hedw.) B.S.G.

AMBLYSTEGIACEAE

Drepanocladus revolvens (Sw.) Warnst.

Drepanocladus uncinatus (Hedw.) Warnst.

Campylium stellatum (Hedw.) C. Jens

ENTODONTACEAE

Pleurozium schreberi (Brid.) Mitt.

BRACHYTHECIACEAE

Brachythecium salebrosum (Web. & Mohr) B.S.G.

Eurhynchium pulchellum (Hedw.) Jenn.

HYLOCOMIACEAE

Hylocomium splendens (Hedw.) B.S.G.

HYPNACEAE

Ptilium crista - castrensis (Hedw.) De Not.

POLYTRICHACEAE

Polytrichum juniperinum Hedw.

LIVERWORTS

LOPHOZIACEAE

Barbilophozia hatcheri (Evans) Loeske

Barbilophozia lycopodioides (Wallr.) Loeske

Barbilophozia sp.

Lophozia sp.

PTILIDIACEAE

Ptilidium pulcherrimum (Web.) Hampe

Blepharostoma trichophyllum (L) Dumort.

PELTIGERACEAE

Peltigera aphthosa (L.) Willd.

Peltigera canina (L.) Willd.

Peltigera leucophlebia (Nyl.) Gyeln.

Peltigera rufescens (Weiss) Humb.

PARMELIACEAE

Cetraria nivalis (L.) Ach.

Cetraria pinastri (Scop.) S. Gray

Hypogymnia enteromorpha (Ach.) Nyl. s. strict.

Hypogymnia physodes (L.) W. Wats.

Parmeliopsis hyperopta (Ach.) Arn.

STICTACEAE

Lobaria linita (Ach.) Rabenh.

CLADONIACEAE

Cladina arbuscula (Wallr.) Hale & W. Culb.

Cladina mitis (Sandst.) Hale & W. Culb.

Cladonia cariosa (Ach.) Spreng.

Cladonia carneola (Fr.) Fr.

Cladonia cenotea (Ach.) Schaer.

Cladonia chlorophaea (Flarke ex Somm.) Spreng.

Cladonia cornuta (L.) Hoffm.

Cladonia cristatella Tuck.

Cladonia deformis (L.) Hoffm.

Cladonia ecmocyna (Ach.) Nyl.

Cladonia fimbriata (L.) Fr.

Cladonia gonecha (Asah.)

Cladonia gracilis (L.) Willd.

Cladonia multiformis Merr.

Cladonia phyllophora Hoffm.

Cladonia pyxidata (L.) Hoffm.

Cladonia sp.

USNEACEAE

Alectoria glabra Mot.

Alectoria sarmentosa (Ach.) Ach.

Usnea scabrata Nyl. ssp. nylanderiana Mot.

STEREOCAULACEAE

Stereocaulon tomentosum Fr. var. tomentosum Fr.

LECANORACEAE

Icmadophila ericetorum (L.) Zahlbr.

Appendix 2. Size class distribution (stems ha^{-1}) and basal area (B.A., m^2 ha^{-1}) of species in the tree strata of habitat types in the Picea glauca Series.

Habitat Type	Stand	Species	B.A. (m2/ha)	Seedlings (31 cm. tall)	Transgressives (31 cm. ht. - 4 cm. d.b.h.)	Saplings 4-8	Diameter Breast Height (cm.) Trees -15	-23	-31	-38	-46	-53	-61	--
Picea glauca/Cornus canadensis-Linnaea borealis	1	Pg*	19	4,000	80	160	160	160	120	160	60			
	5	Pg	1	12,000	160	160	200	20	20	-	-			
		Pc	4	21,000	100	140	60	60	20	-	-			
		Pm	22	-	240	260	240	300	80	-	20			
Picea glauca/Linnaea borealis-Calamagrostis rubescens	7	Pg	21	90,000	400	80	80	160	-	80	-	40	-	-
		Pc	2	600	80	-	-	-	80	-	40	-	-	-
		Pm	33	13,500	-	-	40	-	40	40	40	80	40	40
	10	Pg	10	29,000	7,700	2,160	80	-	-	-	-	-		
		Pc	5	-	1,100	580	120	80	20	-	-	-		
		Pm	15	15,000	1,300	940	120	40	40	40	20	20		
		Sb	-	-	20	20	-	-	-	-	-	-		
		Ac	-	-	20	-	-	-	-	-	-	-		
	14	Pg	3	6,000	300	220	20	20	-					
		Pc	33	2,000	40	200	640	340	60					
		Pm	-	1,000	-	-	40	20	-					
		Pt	1	-	420	-	-	-	-					
Picea glauca/Alnus crispa-Cornus canadensis	13	Pg	1	15,000	60	20	-	-						
		Pc	31	1,000	-	20	760	180						
		Pm	2	2,000	20	-	40	20						
	18	Pgxe	3	11,000	480	500	140	80	20	20	20			
		Al	-	1,000	-	-	-	-	-	-	--			
		Pc	11	1,000	340	1,000	2400	-	-	-	-			
		Mg	-	-	80	-	-	-	-	-	-			
		Sc	-	-	240	-	-	-	-	-	-			
	20	Pgxe	3	4,000	800	240	200	40	20					
		Al	-	-	40	-	-	-	-					
		Pm	-	2,000	140	120	20	-	-					
		Pc	7	12,000	160	80	200	100	-					
		Pt	2	-	6,320	-	-	-	-					
		Ac	-	120	-	-	-	-	-					
		Mg	-	-	40	-	-	-	-					
Picea-Alnus crispa/ Alnus incanus	19	Pgxe	-	16,000	160	60	-	-						
		Pma	-	1,000	140	20	-	-						
		Al	-	7,000	-	20	-	-						
		Pc	17	-	100	2,780	220	40						
		Sb	-	-	120	-	-	-						
		Pt	-	-	240	-	-	-						
	16	Pg	1	1,000	5,960	2,200	-							
		Pma	1	-	1,440	320	-							
		Pc	39	18,000	2,720	17,400	120							
		Pt	1	-	260	-	-							
Picea-Pinus albicaulis/ Juniperus communis/ Alnus incanus	29	Pgxe	14	7,000	40	100	140	80	80	60	-			
		Al	1	1,000	40	40	-	-	-	-	-			
		Pm	2	16,000	-	60	40	-	-	40	20			
		Pa	1	4,000	100	200	60	-	80	-	-			
		Pc	10	1,000	20	260	280	180	80	-	-			
	32	Pe	11	4,500	60	320	140	80	60	60	20			
		Al	2	-	60	40	20	40	20	-	-			
		Pa	5	4,500	640	240	80	80	40	-	-			
		Pc	3	-	200	40	60	60	20	-	-			
		Sg	-	-	-	40	-	-	-	-	-			

Appendix 2. Size class distribution (stems ha^{-1}) and basal area (B.A., m^2 ha^{-1}) of species in the tree strata of habitat types in the Pseudotsuga menziesii Series.

Habitat Type	Stand	Species	B.A. (m^2/ha)	Seedlings (31 cm. tall)	Transgressives (31 cm. ht. - 4 cm. d.b.h.)	Saplings 4-8	Diameter Breast Height (cm.) Trees -15	-23	-31	-38	-46	-53
	2	Pg*	6	4,400	-	80	-	200	20	-		
		Pc	10	3,000	400	180	800	200	20	20		
		Pm	4	1,120	20	40	-	80	20	40		
	8	Pc	19	2,000	280	560	120	400	80	40	-	-
Pseudotsuga menziesii/ [illegible] Calamagrostis purpurascens		Pm	9	7,000	480	280	-	160	40	160	-	160
		Pt	2	-	-	80	-	-	-	-	-	-
	4	Pg	5	20,000	40	100	800	1,400	200	-	-	-
		Pc	7	5,000	40	-	6600	200	-	40	-	-
		Pm	17	30,000	40	120	1,200	1,200	-	20	-	20
	9	Pg	5	17,000	160	80	-	-	-			
		Pc	37	2,000	20	100	2,500	480	60			
		Pm	17	25,000	20	1,180	60	100	-			
		Pt	1	-	-	60	20	20	-			
		Sb	-	-	20	-	-	-	-			
		Ac	-	-	20	-	-	-	-			
	11	Pg	2	900	180	100	40	100	-			
		Pc	21	1,000	80	3,020	260	60	-			
		Pm	4	15,000	140	80	100	40	20			
	12	Pg	-	1,000	-	40	-	-	-	-		
		Pc	23	1,000	80	720	340	120	-	-		
Pseudotsuga menziesii/ Physocarpus malvaceus		Pm	12	38,000	220	480	180	80	20	20		
		Pt	-	-	-	40	-	-	-	-		
	15	Pg	1	-	20	200	20	-	-	-	-	
		Pc	14	1,000	320	420	60	80	80	-	-	
		Pm	4	2,000	60	20	-	20	20	20	20	
		Pt	2	-	120	20	40	20	-	-	-	
		Ac	-	-	60	-	-	-	-	-	-	
	17	Pgxe	2	1,000	200	600	320	120	-	-		
		Pc	23	2,000	1,200	520	640	600	120	40		
		Pm	6	19,000	800	1,280	160	120	-	-		
		Ac	-	40	-	-	-	-	-	-		
		Sb	-	60	-	-	-	-	-	-		

*Species Legend

Trees

Pg = Picea glauca
Pm = Pseudotsuga menziesii
Pc = Pinus contorta
Pt = Populus tremuloides

Trees

Pma = Picea mariana
Pgxe = Picea glauca x engelmannii
Pe = P. engelmannii
Al = Abies lasiocarpa
Pa = Pinus albicaulis

Tall Shrubs

Ac = Alnus crispa
Sb = Salix barratiana
Mg = Menziesia glabella
Sc = Shepherdia canadensis
Ra = Rhododendron albiflorum

Appendix 2. Size class distribution (stems ha^{-1}) and basal area (B.A., m^2 ha^{-1}) of species in the tree strata of habitat types in the Picea engelmanni - Abies lasiocarpa Series.

Habitat Type	Stand	Species	B.A. (m^2/ha)	Seedlings (<31 cm. tall)	Transgressives (31 cm. ht. - 4 cm. dbh)	Saplings	Diameter Breast Height (cm.)									
							Trees									
						4-8	-15	-23	-31	-38	-46	-53	-61	-69	-76	-5-
Picea engelmanni-Abies lasiocarpa Menziesia glabella-Xerophyllum tenax	21	Pgxe	7	2,000	160	340	40	-	-							
		Pma	1	1,000	80	180	-	-	-							
		Al	1	17,000	40	20	40	-	-							
		Pc	12	6,000	400	1,000	60	80	20							
		Ac	2	-	1,420	-	-	-	-							
		Pt	-	-	60	-	-	-	-							
	22	Pgxe	4	12,000	500	520	140	20	-							
		Pma	-	2,000	160	240	20	-	-							
		Al	-	3,000	120	100	-	-	-							
		Pc	4	5,000	240	80	20	40	40							
		Ac	-	-	260	-	-	-	-							
		Mg	-	-	680	-	-	-	-							
		Ra	-	-	100	-	-	-	-							
	23	Pgxe	8	2,000	380	520	360	120	80	40						
		Al	6	13,000	1,800	1,040	280	120	60	20						
		Mg	-	-	520	-	-	-	-	-						
	24	Pe	16	5,000	260	300	80	240	300	80	40					
		Pma	4	2,000	380	720	20	-	-	-	-					
		Al	1	23,000	140	200	80	-	20	-	-					
		Pc	-	-	20	20	-	-	-	-	-					
		Sc	-	-	40	-	-	-	-	-	-					
	25	Pe	10	2,000	40	40	60	120	100	20	40	20	20			
		Pma	1	-	140	160	40	-	-	-	-	-	-			
		Al	8	13,000	1,780	660	300	120	20	20	-	-	-			
		Mg	-	480	-	-	-	-	-	-	-	-	-			
	27	Pe	17	5,000	320	320	140	100	40	20	20	20	20	20		
		Pma	-	7,000	60	20	-	-	-	-	-	-	-	-		
		Al	13	47,000	1,420	600	280	80	60	20	-	-	-	-		
		Pc	1	-	60	60	40	20	20	-	-	-	-	-		
		Mg	-	-	240	-	-	-	-	-	-	-	-	-		
		Sc	-	-	60	-	-	-	-	-	-	-	-	-		
Picea engelmanni-Abies lasiocarpa/Arnica cordifolia	28	Pe	29	7,000	400	520	200	80	360	200	200	120	120	120		
		Pma	1	1,000	360	200	80	-	-	-	-	-	-	-		
		Al	13	19,600	800	480	320	240	40	40	-	-	-	-		
	30	Pe	18	5,000	1,920	960	400	600	600	200	160	200	40	20	20	20
		Pma	1	2,000	200	100	20	-	-	-	-	-	-	-	-	-
		Al	18	30,000	3,800	1,080	400	400	200	120	-	-	-	-	-	-
Picea engelmanni-Abies lasiocarpa/Arnica cordifolia/Hylocomium splendens	31	Pgxe	4	-	360	360	120	40	80	-	140	-	40	40		
		Al	1	6,000	80	80	80	-	-	-	-	-	-	-		
		Pa	3	3,000	780	180	-	80	60	-	-	20	-	-		
		Pc	3	-	-	20	-	20	-	40	-	-	-	-		
	33	Pe	3	400	280	40	100	60	60	-	40	40	20	-	20	
		Al	11	130,000	17,000	4,040	400	180	100	20	-	-	-	-	-	

Appendix 3. Similarity index matrix using Sorenson's (1948) Coefficient o

The Coefficients are converted to a percentage (x 100) and th
of dissimilarity.

STANDS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2	2.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
3	1.3	22.5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
4	20.0	38.7	10.1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5	19.7	17.5	2.1	28.9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
6	0.4	25.9	26.6	10.6	7.3	.	.	.	.	.	.	.	.	.	.	.	.	.	.
7	22.1	6.5	11.3	26.7	19.4	4.3	.	.	.	.	.	.	.	.	.	.	.	.	.
8	5.6	27.8	8.7	42.5	24.1	14.3	20.7	.	.	.	.	.	.	.	.	.	.	.	.
9	20.4	10.5	2.7	26.8	28.4	3.6	23.5	21.8	.	.	.	.	.	.	.	.	.	.	.
10	21.5	10.0	0.7	17.0	23.5	8.0	18.5	12.6	21.5	.	.	.	.	.	.	.	.	.	.
11	6.2	7.9	3.0	13.5	24.8	13.1	10.9	18.1	24.1	15.6	.	.	.	.	.	.	.	.	.
12	7.1	5.9	0.7	28.1	26.9	3.2	11.9	25.5	21.1	14.4	22.4	.	.	.	.	.	.	.	.
13	15.0	9.4	1.6	18.2	20.2	1.0	23.4	18.3	32.7	12.0	11.4	9.2	.	.	.	.	.	.	.
14	21.3	6.6	1.1	8.0	21.5	1.2	14.0	17.4	17.4	13.6	9.9	9.5	30.4	.	.	.	.	.	.
15	7.6	11.1	14.8	14.7	22.4	2.3	11.9	23.0	28.0	13.2	25.5	18.4	21.0	17.9	.	.	.	.	.
16	6.3	7.2	3.1	7.9	13.7	4.4	17.2	10.5	16.5	10.2	6.9	5.7	25.1	18.5	13.4	.	.	.	.
17	10.1	14.7	10.5	24.5	23.2	6.0	18.5	26.9	26.8	13.3	6.9	11.0	31.8	15.6	19.0	16.8	.	.	.
18	13.3	1.3	0.2	14.3	23.1	0.4	18.0	17.6	15.0	11.3	15.4	21.7	21.0	21.8	12.9	15.8	12.4	.	.
19	7.1	2.1	1.8	13.8	15.5	0.6	11.0	7.3	16.8	10.2	9.5	16.9	19.9	16.8	15.6	15.5	14.3	32.6	.
20	8.3	4.2	1.3	8.7	25.1	4.6	8.1	9.7	13.3	7.4	13.4	9.2	23.5	18.6	12.4	14.6	14.2	23.7	24.0
21	14.1	6.0	3.3	10.0	8.3	3.2	15.6	10.4	11.7	7.6	12.9	6.0	20.9	17.9	12.6	24.6	10.9	24.5	12.6
22	7.2	1.6	1.4	8.4	4.8	0.4	11.4	10.4	5.9	4.2	9.3	12.0	7.2	11.0	5.6	11.4	3.9	42.8	20.4
23	11.2	3.2	0.3	5.8	12.3	0.6	11.5	4.2	4.7	12.7	3.7	4.1	7.5	13.8	4.8	7.3	4.9	10.7	12.8
24	13.1	6.1	1.5	11.1	22.0	4.7	15.8	8.8	16.2	15.6	5.0	7.2	14.0	24.8	6.7	9.6	12.1	14.9	9.9
25	21.8	1.7	0.1	9.0	16.4	0.4	13.8	4.9	6.9	13.7	8.7	3.7	10.6	24.5	7.4	8.4	4.3	34.9	10.9
26	2.8	0.4	2.9	0.2	4.7	3.7	2.0	3.1	4.1	2.5	3.2	2.4	3.9	3.4	4.4	4.2	6.2	3.2	5.7
27	12.5	0.2	0.1	8.4	14.4	0.2	13.4	3.8	4.9	17.9	2.4	3.1	10.3	17.7	5.3	9.8	4.3	16.7	11.2
28	13.0	0.1	0.2	8.8	13.1	0.3	17.6	6.3	7.3	14.0	4.5	5.9	15.7	21.3	6.3	10.6	12.8	16.9	9.6
29	3.4	16.1	3.5	19.6	15.2	10.2	6.1	24.2	13.6	15.8	5.2	21.8	15.2	13.7	13.2	10.2	18.3	11.0	13.9
30	12.6	1.2	0.1	12.5	8.5	0.1	14.5	6.6	1.7	8.8	15.7	7.9	9.5	12.5	0.9	7.9	2.1	13.3	6.3
31	6.2	3.0	4.3	4.9	4.7	0.7	10.0	3.1	5.2	13.8	0.5	4.8	6.9	11.7	3.8	3.4	5.2	19.2	10.1
32	7.7	13.0	2.9	16.1	15.7	10.1	8.9	18.7	14.1	8.9	6.9	12.4	12.3	10.5	15.4	8.8	16.7	13.6	16.0
33	7.9	0.1	0.1	8.8	6.1	0.1	10.0	2.4	3.7	4.8	19.3	1.1	4.5	6.2	2.1	12.2	1.7	7.7	4.1
34	0.6	0.6	0.2	0.1	0.1	0.1	1.0	1.0	0.4	0.1	0.9	0.5	0.7	0.1	1.9	3.4	2.1	0.5	0.4
35	0.5	0.6	0.2	0.7	0.1	0.2	0.2	0.9	0.4	3.0	0.1	2.5	1.4	0.0	1.6	0.9	2.6	1.2	0.3
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19

ix using Sorenson's (1948) Coefficient of Community: $\frac{2W}{a+b}$ (Index of similarity)
converted to a percentage (x 100) and then subtracted from 100 to obtain the index

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STANDS

13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
30.4																						
21.0	17.9																					
25.1	18.5	13.4																				
31.8	15.6	19.0	16.8																			
21.0	21.8	12.9	15.8	12.4																		
9.9	16.8	15.6	15.5	14.3	32.6																	
3.5	18.6	12.4	14.6	14.2	23.7	24.0																
0.9	17.9	12.6	24.6	10.9	24.5	12.6	28.7															
7.2	11.0	5.6	11.4	3.9	42.8	20.4	24.5	33.4														
7.5	13.8	4.8	7.3	4.9	10.7	12.8	9.1	20.2	24.8													
4.0	24.8	6.7	9.6	12.1	14.9	9.9	13.4	14.8	15.6	19.7												
0.6	24.5	7.4	8.4	4.3	34.9	10.9	14.7	20.2	23.4	35.2	32.1											
3.9	3.4	4.4	4.2	6.2	3.2	5.7	8.8	2.0	2.7	1.0	10.2	4.5										
0.3	17.7	5.3	9.8	4.3	16.7	11.2	13.3	17.4	16.3	30.9	29.5	40.3	2.0									
3.7	21.3	6.3	10.6	12.8	16.9	9.6	12.9	23.7	12.4	24.0	23.6	31.7	4.0	26.7								
5.2	13.7	13.2	10.2	18.3	11.0	13.9	17.5	14.5	6.0	6.8	19.4	7.0	3.1	10.0	6.4							
9.5	12.5	0.9	7.9	2.1	15.3	6.3	8.9	12.7	23.6	33.2	18.7	26.3	4.2	20.5	41.0	4.5						
6.9	11.7	3.8	3.4	5.2	19.2	10.1	4.5	5.9	15.4	12.9	11.7	17.6	7.3	7.3	16.7	15.9	12.1					
2.3	10.5	15.4	8.8	16.7	13.6	16.0	14.4	11.1	9.8	6.4	8.8	4.9	7.3	8.3	4.3	49.1	2.0	15.8				
4.5	6.2	2.1	12.2	1.7	7.7	4.1	5.3	13.4	15.9	8.1	12.1	9.1	1.1	9.3	9.2	3.4	11.2	4.5	2.9			
0.7	0.1	1.9	3.4	2.1	0.5	0.4	0.2	1.1	2.9	2.0	8.8	1.2	16.6	0.2	3.1	3.9	2.3	3.0	0.7	7.0		
1.4	0.0	1.6	0.9	2.6	1.2	0.3	0.4	0.6	2.4	1.5	1.8	1.2	8.3	0.3	1.5	1.8	1.9	3.3	0.7	8.6	20.4	
13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35

Appendix 4. Physical Properties of soils samples from all stands.
(C = clay, Si = silt, S = sand, L = loam).

STAND	HORIZON	COLOR (dry)	% C	% Si	% S	TEXTURE
1	A	Lt. brownish gray (10 YR 6/2)	26	26	48	SCL
	C	Brown (10 YR 5/3)	14	24	62	SL
2	A	Brown (10 YR 5/3)	5	35	60	SL
	B	Brownish yellow (10 YR 6/8)	9	25	66	SL
	C	Lt. gray (10 YR 7/2)	10	23	77	SL
3	A	Pale brown (10 YR 6/3)	33	28	38	CL
	C	White (10 YR 8/2)	25	27	48	SCL
4	A	Lt. yellowish brown (10 YR 6/4)	19	23	58	SL
	B	Dk. yellowish brown (10 YR 4/4)	11	35	54	SL
	C	White (10 YR 8/1)	67	26	6	C
5	A	Yellowish brown (10 YR 5/6)	25	34	40	L
	B	Very pale brown (10 YR 7/4)	18	72	60	SL
	C	Lt. gray (10 YR 7/1)	15	43	42	L
6	A	Grayish brown (10 YR 5/2)	-	-	-	-
	C	Lt. brownish gray (10 YR 6/2)	19	21	50	SL
7	A	Dk. brown (10 YR 4/3)	9	20	70	SL
	B	Lt. gray (10 YR 7/2)	39	27	34	CL
	C	Lt. gray (10 YR 7/2)	41	29	30	C
8	A	Lt. yellowish brown (10 YR 6/4)	11	25	64	SL
	B	Strong brown (7.5 YR 5/6)	7	20	72	SL
	C	Grayish brown (10 YR 5/2)	9	29	62	SL
9	A	Very pale brown (10 YR 8/4)	11	54	34	SiCL
	B	Brownish yellow (10 YR 6/8)	33	28	38	CL
	C	Very pale brown (10 YR 7/3)	19	22	58	SL

Appendix 4. Con't.

STAND	HORIZON	COLOR (dry)	% C	% Si	% S	TEXTURE
10	A	Yellow (10 YR 7/6)	19	27	54	SL
	B	Yellow (10 YR 7/6)	27	10	62	SCL
	C	Lt. gray (10 YR 7/2)	16	32	52	SL
11	A	Yellowish brown (10 YR 5/6)	21	26	50	SCL
	B	Brownish yellow (10 YR 6/8)	20	26	56	SCL
	C	Very pale brown (10 YR 7/4)	13	32	54	SL
12	A	Yellowish brown (10 YR 5/8)	12	40	48	SL
	B	Yellowish brown (10 YR 5/4)	15	41	44	L
	C	Very pale brown (10 YR 7/4)	13	19	68	SL
13	A	Brownish yellow (10 YR 6/6)	27	22	51	SCL
	B	Brownish yellow (10 YR 6/6)	21	23	55	SCL
	C	Pale brown (10 YR 6/3)	17	28	54	SL
14	A	Yellow (10 YR 7/6)	24	45	31	L
	B	Lt. gray (10 YR 7/2)	19	23	58	SL
	C	Brownish yellow (10 YR 6/6)	27	27	46	SCL
15	A	Yellow (10 YR 7/6)	9	46	44	L
	B	Brownish yellow (10 YR 6/6)	23	28	49	SCL
16	A	Brown (10 YR 5/3)	23	42	36	L
	B	Brownish yellow (10 YR 6/8)	19	43	38	L
	C	Lt. yellowish brown (10 YR 6/4)	9	13	78	LS
17	A	Brownish yellow (10 YR 6/6)	31	27	42	SCL
	B	Pale brown (10 YR 6/3)	15	23	62	SL
	C	Lt. gray (10 YR 7/2)	22	26	52	SCL
18	A	Brownish yellow (10 YR 6/8)	27	22	42	SCL
	C	Lt. yellowish brown (10 YR 6/4)	13	26	52	SL
19	A	Very pale brown (10 YR 7/4)	27	53	20	CL
	B	Lt. gray (10 YR 7/2)	20	34	26	L
	C	Pale brown (10 YR 6/3)	17	39	44	L

Appendix 4. Con't.

STAND	HORIZON	COLOR (dry)	% C	% Si	% S	TEXTURE
20	A	Very pale brown (10 YR 7/4)	18	37	45	L
	B	Yellowish brown (10 YR 5/6)	20	22	59	SL
	C	Brownish yellow (10 YR 6/6)	15	15	70	SL
21	A	Grayish brown (10 YR 5/2)	6	27	67	SL
	C	Lt. yellowish brown (10 YR 6/4)	11	31	58	SL
22	A	Very pale brown (10 YR 7/4)	39	37	24	CL
	B	Brownish yellow (10 YR 6/6)	20	30	51	SCL
	C	Yellowish brown (10 YR 5/6)	11	18	70	SL
23	A	Yellowish brown (10 YR 5/4)	11	48	41	L
	B	Yellowish brown (10 YR 5/6)	12	25	63	SL
	C	Brownish yellow (10 YR 6/6)	16	42	42	L
24	A	Dk. brown (10 YR 3/3)	9	36	55	SL
	B	Lt. brownish gray (10 YR 6/2)	16	39	46	L
	C	Lt. yellowish brown (10 YR 6/4)	13	19	68	SL
25	A	White (10 YR 8/2)	16	53	32	L
	B	Yellowish brown (10 YR 5/6)	24	39	37	L
	C	Dk. brown (10 YR 4/3)	17	44	39	L
26	A	Very dk. gray brown (10 YR 3/2)	20	52	28	L
	C	Dk. grayish brown (10 YR 4/2)	19	48	33	SiL
27	A	Pale brown (10 YR 6/3)	16	35	49	L
	B	Lt. brownish gray (10 YR 6/2)	14	31	55	SL
	C	Dk. yellowish brown (10 YR 4/4)	17	27	54	SL
28	A	Lt. brownish gray (10 YR 6/2)	46	39	15	C
	B	Very dk. gray brown (10 YR 3/2)	19	35	46	L
	C	Dk. brown (10 YR 4/3)	21	30	48	L
29	A	Yellow (10 YR 7/6)	14	48	38	L
	C	Brownish yellow (10 YR 6/8)	16	42	42	L

Appendix 4. Con't.

STAND	HORIZON	COLOR-(dry)	% C	% Si	% S	TEXTURE
30	A	Lt. yellowish brown (10 YR 6/4)	17	46	36	SiL
	B	Yellow (10 YR 7/6)	24	41	36	L
	C	White (10 YR 8/2)	19	38	42	L
31	A	Lt. gray (10 YR 7/1)	14	36	50	SL
	C	Lt. yellowish brown (10 YR 6/4)	8	44	48	L
32	A	Very pale brown (10 YR 8/3)	46	39	15	LC
	C	Dk. brown (10 YR 3/3)	15	44	41	L
33	A	Pale brown (10 YR 6/3)	12	45	43	L
	B	Dk. brown (10 YR 3/3)	13	43	44	L
	C	Dk. brown (7.5 YR 3/2)	12	40	48	L
34	A	Dk. brown (10 YR 4/3)	39	37	24	CL
	B	Brownish yellow (10 YR 6/6)	27	53	20	CL
	C	Lt. yellowish brown (10 YR 6/4)	25	42	33	L
35	A	Dk. brown (10 YR 4/3)	21	44	34	SiL
	B	Brownish yellow (10 YR 6/6)	14	35	52	L
	C	Lt. yellowish brown (10 YR 6/4)	22	29	49	SCL
36	A	Dk. brown (10 YR 3/3)	15	45	40	L
	C	Gray (10 YR 6/1)	7	41	52	SL
	A	Yellowish brown (10 YR 5/4)	12	42	46	L
	C	Gray (10 YR 6/1)	8	38	54	SL

Appendix 5. Chemical analysis of soil samples from selected stands. Samples are composites of both soil pits. Not all horizons were samples in each stand.

Stand	Horizon	PPM N_2	PPM P^{++}	PPM K^{+}	PPM Na^{+*}	PPM S^{*}	Free Lime* $CaCO_3$	Soil Reaction pH
2	A	4	6	185	-	-	0	7.7
	B	2	4	128	-	-	2	8.0
	C	6	-	40	-	-	8	7.9
4	A	1	-	272	1	5	9	7.4
	B	1	-	77	1	6	9	7.8
	C	1	-	82	1	-	9	8.0
6	A	2	-	62	2	6	9	8.4
	C	1	-	60	2	-	9	8.6
7	A	9	5	75	1	8	9	6.8
	B	7	-	122	1	5	9	8.0
	C	4	-	100	1	-	9	8.0
8	A	2	8	95	1	2	7	7.6
	C	-	-	17	1	3	7	9.0
10	A	-	-	142	-	4	9	7.0
	C	-	-	60	1	-	9	7.8
12	A	-	8	110			9	8.2
	C	-	8	90			9	8.6
16	A	-	4	106	1	5	9	6.7
	B	-	-	50	1	4	9	7.6
	C	2	-	50	1	-	9	7.7
17	A	-	-	140	1	5	9	7.2
	B	-	-	57	1	4	9	7.5
	C	-	-	48	1	-	9	7.8

* Amount based on an index where 2 = Low, 5 = Medium, 8 = High.

Appendix 5. Con't.

Stand	Horizon	PPM N_2	PPM P^{++}	PPM K^{+}	PPM Na^{++}	PPM S^{*}	Free Lime* $CaCO_3$	Soil Reaction pH
20	A	-	-	35	1	4	2	6.2
	B	2	-	55	1	5	9	7.5
	C	1	-	35	1	-	9	7.8
22	A	17	3	60	1	5	4	5.2
	B	3	-	40	2	5	9	7.8
	C	5	1	45	1	2	9	7.9
23	A	3	2	55	1	-	-	4.7
	B	3	-	35	1	6	-	6.3
	C	2	-	40	1	8	9	7.6
26	A	11	6	150	1	2	3	7.6
	C	50	10	430	1	3	9	7.1
27	A	1	-	42	1	6	-	6.7
	B	25	2	55	1	8	-	7.1
	C	6	-	42	1	-	9	7.5
30	A	4	7	35	2	6	-	5.8
	B	2	5	30	1	4	-	5.6
	C	4	-	45	1	-	9	7.7
32	A	6	-	60	1	6	-	7.3
	C	18	10	32	1	6	-	6.0
34	A	13	8	47	1	8	0	5.6
	B	7	5	40	1	8	0	6.3
	C	2	-	45	1	4	8	7.8
36	A	40	27	37	1	9	-	6.6
	C	3	25	70	2	6	2	7.2

Appendix 6. Example of the morphological cone scale index to assess the stand position on the Picea glauca - P. intermediate - P. engelmannii gradient. The index is that of Horton (1959) which was also used by Beil (1966) in the study area vicinity. The placement of the characters into classes is qualitative. As explained by Horton (1959), P. engelmannii characters are; 1) An erose, pointed cone scale apex, 2) The widest part of the scale near the middle and the scale wedge-shaped, 3) Thin, flexible cone scale. P. glauca characteristics are; 1) A rounded smooth apex, 2) The widest part of the scale, 1/3 of the total length back from the apex, 3) stiff cone scales. The data from stand 25 are used as an example for calculating a stand index value.

	Index 0	1	2	3	4
Apex Shape			13	18	20
Widest Part of Scale			14	17	20
Scale Stifness			13	19	19
Σ Class			40	54	59
% Total			26	35	39
% x Index			52	105	156

Stand Index Value = 313 out of a possible range of 0-400.